ECOLOGICAL MONOGRAPHS

VOL. 8 JANUARY, 1938 No. 1

PLANT COMMUNITIES IN THE MARSHLANDS OF SOUTHEASTERN LOUISIANA

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PLANT COMMUNITIES IN THE MARSHLANDS OF SOUTHEASTERN LOUISIANA

INTRODUCTION

The marshlands of Louisiana include large interrupted areas of fresh water marsh and a vast, practically unbroken expanse of brackish and salt-water marsh along the coast. This saline "wet prairie" forms a part of the still greater body of marsh vegetation which extends from Maine to Texas. Since Louisiana includes over four million acres of marshlands we resolved to inspect a considerable number of marsh areas in the southern part of the state and to conduct routine monthly studies on marsh habitats within a day's journey from New Orleans.

This study has involved 23 reconnaissance trips, 66 monthly visits to seven transects made during one annual cycle, and about twenty confirmatory trips subsequent to the routine investigation. On each trip we noted, so far as possible, the relative abundance and phenology of each species in every community of the transect visited. Of the habitat factors we determined water level, salinity of surface water and soil water, and also the water content and organic matter in the upper 2 feet of soil. Although our quantitative data were obtained only from marshlands in the vicinity of New Orleans we believe that they represent in a general way conditions throughout the Gulf Coastal Plain. The work has now been in progress for more than 4 years. During that time we have had the loyal co-operation of numerous assistants in the departments of Botany and Zoology of Tulane University, and we gratefully recognize their valuable contributions to the study.

Historical

As early as 1903 Ganong described the salt marshes of the Bay of Fundy and the effects of dikes on the marsh vegetation. An interesting account of the New Jersey marshes was given by Smith in 1907. He divided the salt marshes into those that are covered by each high tide, those covered only by the highest tides and those which are rarely covered by any except the most extreme storm tides. He briefly indicated the succession of the important species, gave a meager account of the edaphic factors, and discussed the economics of the marshes. In addition he showed that the marshes degrade and sink if the salt water is excluded and advised ditching to the sea as a method of marsh improvement and mosquito control. A more complete description of the vegetation of the salt marshes of New Jersey was given by Harshberger (1909). In this paper the author also discussed the transition from fresh water to brackish water marshes and made an attempt at correlating the distribution of salt marsh vegetation with the salinity of soil water.

Johnson and York (1915) described the littoral vegetation at Cold Spring Harbor and correlated vegetation with substratum, currents, tides, and salinity. They suggested that, in any region, the vertical range of a littoral plant would be exactly proportional to the range of the tide. In the New Jersey marshes the formation of salt marsh pools, from a few feet across to an acre or more in extent, is fairly common (Harshberger, 1916). These pools were shown to be due to the rapid decay of both aerial and subterranean parts of vegetation which is covered by tide-carried rafts of vegetable débris. The problem of bank softening and soil shrinkage due to exclusion of salt water was further elaborated by Rudolphs (1926). He also showed that bald spots in the marshes were due to excessive salinity (up to 22.2 percent salt) and that these spots revegetated very slowly. Emphasis was placed on the saline hydroperiod as a major factor in the delimitation of salt marsh communities in North Carolina by Wells (1928). He also listed the important species in each community and indicated their successional relations.

Of the studies in the Gulf Coastal States the early work of Mohr (1901) is significant. In it he described the relatively fresh water marshes of the Mobile River estuary and the littoral marshes of the coast which he designated as the "southern juncaceous formation." Lowe (1919, 1921) discussed the geology and soils of the Mississippi marshes, especially of Pascagoula and Mobile bays, and listed the predominant marsh species. In the South Atlantic and Gulf States there are 5,600,000 acres of salt marshes and of this area 3,381,500 acres are located in Louisiana (Griffitts, 1928). Louisiana has the doubtful honor of having nearly twelve times as much salt marsh as New Jersey and almost half the total salt marsh area of the Atlantic and Gulf coasts.

In his work on the fur animals of Louisiana Arthur (1931) included much that is of value to the plant ecologist. He indicated the beneficial effect of humus and the harmful effects of drought and fire on muskrat production in the Louisiana marshes. Viosca (1928) in discussing the physiography of the Louisiana wetlands indicates that of the total area of Louisiana nearly one-third (10,000,000 acres) is given over to swamps, marshes, or open water. He includes a good discussion of the biotic interrelations in the marshes and makes an impassioned plea for the restoration of natural conditions which are best suited to an abundant marsh flora and fauna. In a discussion of the vegetation of Cat Island, Mississippi, Penfound and O'Neill (1933) described the communities of both fresh and brackish water marshes, and indicated their successional relations. They also gave physical data which, though meager, suggested that the water table and the salinity of the soil were of the utmost importance in the delimitation and composition of marsh communities.

Of the investigations of the salt deserts of the western United States

those of Kearney (1914) and Flowers (1934) are outstanding. In his study of the vegetation of Tooele Valley, Utah, Kearney described the salt flat communities, indicated their successional relations and their dependence on salinity and soil moisture. In both of the above investigations the marshes, as described, are very different from those of the Atlantic and Gulf coasts. In fact, Flowers lists only eleven spermatophytes common to the Great Salt Lake marshes and the salt marshes of Louisiana. Of the salt marsh species salt grass *(Distichlis spicata*[1]*)*, is classed by him as the most versatile, successful and salt tolerant plant of the region. In both investigations salinity determinations were based on the dry weight of the soil. In spite of this fact Flowers states that "the real feature of significance is the concentration of the soil solution." Since we have determined only the salinity of the surface water and that of the soil solution no comparisons are possible between their data and our results in the Louisiana marshes.

Several of the more recent papers on marshes have dealt with salinity relations. Alexander et al (1932) showed that the salinity of the soil water was usually higher and fluctuated less than that of the surface water in the estuary of the Tees River. Nicol (1935) confirmed these results and demonstrated that the interchange of salt between mucky soils of pools and the superposed surface water was very slow. It was pointed out by Steiner (1934) that the osmotic pressure of the soil solution of the marsh soils decreased with depth to a point about 12 to 15 inches below the soil surface. Since the root level of marsh plants was also found by him to vary with the species it is evident that autecological studies are necessary in order to understand the water economy of halophytic plants. These and other problems concerning halophytes are summarized by Chapman (1936).

CLIMATE

The areas under investigation are all situated within 70 miles of New Orleans in southeastern Louisiana. The New Orleans area possesses an essentially semi-tropical and coastal climate because of its latitude (30° North) and its proximity to the Mississippi River, to Lakes Pontchartrain, Borgne, and Salvador, and to the Gulf of Mexico. The nature of the climate is indicated by the data in Table 1, which are taken from the reports of the

TABLE 1. GENERAL METEOROLOGICAL CONDITIONS, 1932, 1933, AND NORMAL (LONG TERM AVERAGE)

	Temperature mean annual	Rainfall *inches*	Relative humidity (12 M)	Sunshine *percentage*	Wind direction	Growing season
1932	70.3°	72.12	61	61	Northeast	278
1933	72.1°	48.49	58	62	Southeast	345
Normal	69.4°	59.34	63	58	Southeast	326

[1] The "Manual of the Southeastern Flora" by Small (1933) has been closely followed in nomenclature.

United States Weather Bureau, kindy furnished by the New Orleans office. The mean annual temperature is 69.4°F. with mean monthly temperatures of 54.6°F. for January and 82.4°F. for July. Precipitation is quite evenly distributed throughout the year with July and August as the wettest months and October and November as the driest. Despite the considerable annual rainfall (59.34 inches) and the high relative humidity (63 percent at 12 M.) the amount of sunshine (58 percent of possible) is not far below the average for the Mississippi valley. Since there are few severe frosts and since the frostless season is 326 days, some species are found in bloom every day of the year.

Our detailed studies on the transects were started in February, 1932, the warmest February of record and with very low rainfall (Fig. 1). It

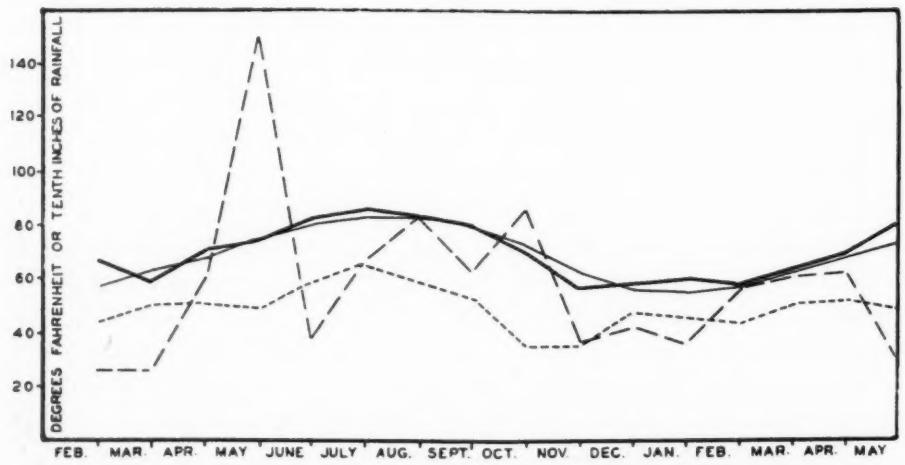

FIG. 1. Monthly temperatures (heavy solid line) and monthly rainfall (broken line) during period of investigation compared with mean monthly temperatures (light solid line) and mean monthly rainfall (dotted line).

was preceded by two months also characterized by high temperatures but with abundant rainfall. The average temperature for the year was 1.0°F. above the normal and the total rainfall for the year was 14.53 inches above the long term average, with a maximum excess of 15.06 inches in May. Despite the shorter frostless season (278 days) the weather in 1932 was very favorable to the development of vegetation as well as mosquitoes, and was generally acclaimed as an unusually bad mosquito year. The weather of the first five months of 1933 was not greatly different from the long period average. The average temperature for the same period (66.4°F.) was 2.7°F. higher than the normal (63.7°F.), but the average monthly rainfall (4.95 inches) was only 0.11 inch greater than the long term average (Fig. 1). Since other climatic conditions were typical the last five months of the period of investigation were especially favorable to the development of vegetation.

PHYSIOGRAPHIC CONDITIONS

The marshes of southeastern Louisiana include approximately one and three-quarter million acres of fresh water marsh and about two and one-half million acres of sea marsh (Viosca, 1928). The fresh water marshes occur in large interrupted areas in the interior of the state, but the salt marshes occupy a practically unbroken strip of coastline several miles in width (Fig. 2). Some of the marshes occur in or adjacent to the Gulf Coastal

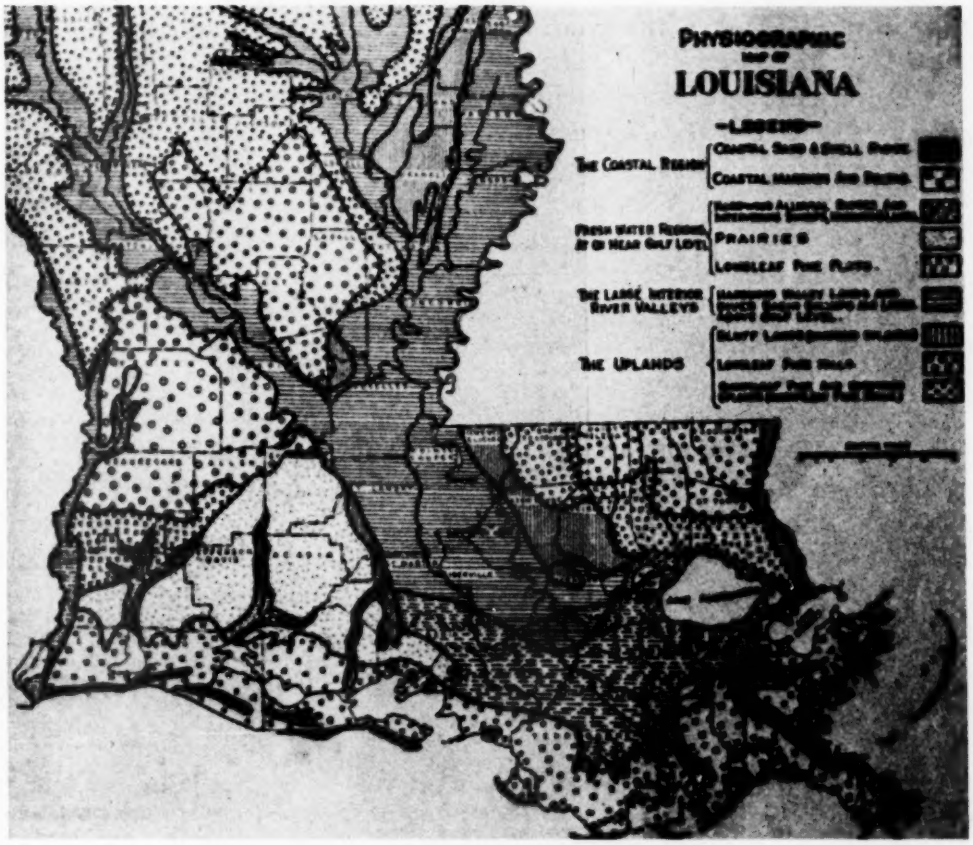

FIG. 2. Physiographic map of Louisiana.

Plain but most of the marsh area under investigation is situated in the lower Mississippi delta below Lake Pontchartrain. The sediments of the Gulf Coastal Plain are of comparatively recent marine origin and, except in the flood plains of the longer dissecting streams, are usually acid in reaction. The Mississippi delta in southeastern Louisiana is still more recent in origin but is characterized, especially near the coast, by soils which are typically alkaline in reaction.

In the Mississippi alluvial plain the river now has no tributaries below St. Francisville, and aside from the present passes at the mouth of the Mississippi there are no active distributaries except the Atchafalaya River.

But in the past there were several outlets which either have been naturally abandoned by the parent stream or closed off by levee builders. These distributaries issued from the Mississippi or the Atchafalaya, and by branching formed a fan-shaped delta of great extent (Fig. 2). The varying topography of the Mississippi alluvial plain is the result of uneven deposition of sediments by these different distributaries.

In general the region under investigation is an extensive alluvial plain with little relief which dips slightly gulfward and approximates sea level throughout the lower portion. Each deltaic stream included within this alluvial plain is flanked by natural levees, popularly called "front lands," which are formed by the deposition of the coarser sediments during flood periods. The elevation of these natural levees gradually decreases away from the stream front to the so-called "back lands" or "black lands" which differ from the front lands in the finer texture and darker color of their soils. Where the back lands dip below the mean water table they are occupied by cypress-gum swamps and marshes in fresh water areas but only by marshes in more saline areas. These wetlands do not drain into the main streams but are merely catch basins for the overflow waters and for rainfall in the alluvial plain. These catch basins are drained by sluggish, meandering bayous, characterized by insignificant levees and designated as "swamp drainage bayous" by Viosca (1933). In addition there are occasional elongated or nearly circular "islands" which vary from a few inches to several feet above the surrounding marshes. Most of these, especially in southwestern Louisiana, are former barrier beaches although others appear to be outlying fragments of the Gulf Coastal Plain. Whenever one of these elevations is clothed with evergreen oaks it is termed a *chênière*.

TRANSECT STUDIES

Location of Transects

In attempting to locate representative areas, marshes from Cat Island, Mississippi, westward to East Cote Blanche Bay, and from Lake Pontchartrain southward to Grand Isle and the Passes at the mouth of the Mississippi River were visited. The preliminary survey, involving a total of 23 trips, revealed a surprising diversity in the composition of these "wet prairies." Our plan was to include areas of varying degrees of salinity from fresh water areas to the most saline habitat, but near enough to New Orleans to permit routine investigation. We were also interested in locating marshes which were essentially untouched by man. This required a prolonged reconnaissance which necessitated some difference in time in locating proper stations. However seven transects were finally established within a radius of 70 miles from Tulane University, New Orleans (Fig. 3).

The fresh water marsh transect is situated near Raceland in the Lake Des Allemands drainage area. This transect, hereafter called the Raceland

FIG. 3. Location of transects near New Orleans.

transect, is just south of the Old Spanish Trail (U. S. 90) 36 miles southwest of New Orleans. A nearly fresh water area (less than 0.5 percent salt) known as the Slidell transect was selected near Slidell on U. S. 90 some 43 miles northeast of New Orleans, at the junction of the Pearl River delta and the Gulf Coastal Plain.

Three transects were located in brackish marsh areas (0.5-2.0 percent salt). The Bayou Villars transect (0.3-1.0 percent salt) is situated near the confluence of Bayou Villars and Bayou Barataria in the Mississippi Alluvial Plain on Louisiana Highway 30 (Fig. 3). A special feature of this transect is a swamp of bald cypress in which the trees of the forest-marsh ecotone are dwarfed and scraggly. A second brackish station known as the Oak Island transect (0.8-1.4 percent salt) was established on the northwestern border of an "island" of live oaks *(chênière)* in the Pearl River Alluvial Plain, approximately 40 miles northeast of New Orleans on U. S. Highway 90. This transect is characterized by the absence of cypress trees probably due to the relatively high salinity of the area. The third, known as the Foster transect (0.6-1.7 percent salt), is situated on Grand Bayou near the Foster Packing Plant about 45 miles south of New Orleans on Louisiana Highway 31.

The two saline stations are also located on Grand Bayou, but well toward the Gulf of Mexico (Fig. 3). The Yellow House transect was laid out in a marsh of much higher salinity (3.3-3.7 percent salt) west of Empire, some 60 miles south of New Orleans on Louisiana Highway 31. This transect was established on the western shore of Grand Bayou 1.5 miles below its confluence with Mevers Canal and approximately 8.5 miles from Empire (Fig. 3). The Popich transect (3.5-4.5 percent salt) is 3 miles south of the Yellow House transect on the eastern shore of the Bayou across from an oyster camp owned by Mr. Joseph Popich. The unique character of this transect is the presence of a honey mangrove community along the front lands of the bayou.

METHODS OF INVESTIGATION

Our plan was to study each of the seven transects, once a month, throughout an annual cycle. On each trip, so far as practicable, the relative abundance and phenology of each species of plant and animal in every community of the transect were noted. Of the habitat factors the writers observed the depth of the surface water (where present) and collected surface water from the marsh and water from adjacent bayous or lagoons for the determination of salinity. In addition soil samples were obtained from the first and second feet of soil by means of a soil auger for the determination of water content and percentage of organic matter (Fig. 4). After allowing the water in the hole to attain a constant level, the position of the water, with reference to the soil surface, was ascertained and a quart sample was procured for the determination of salinity. The amount of slope within each transect was determined by comparing the water levels in the various zones during periods of high water, when the transects were largely or wholly submerged.

VEGETATION OF THE TRANSECTS

Each transect was started on an elevation and was projected across the typically gradual slope to the extensive paludal basins away from the ridge.

FIG. 4. Equipment utilized in marsh studies.

The elevations and a major portion of the slopes are characterized by a water level below the soil surface whereas the basins usually have standing water. In relatively fresh water areas the elevations, if of sufficient height, are occupied by pine or oak forests which are separated by a cypress-gum swamp from the marshes in the basins (Table 2). In brackish or saline areas with similar elevations the cypress-gum swamp is eliminated and the oak forest is now fringed by one or more zonal communities (where the average water level is below the soil surface) beyond which lies the usually extensive marsh (characterized by standing water). *It should be emphasized also that the transition from one community to another is conditioned by a change in elevation of as little as 3 inches since four communities may occur on a slope having a fall of less than 1 foot.*

The transects studied include 11 distinctly different communities of which three are forests, four are zonal associes and four are true marshes of considerable extent. In addition, there are several consocies which are correlated with local differences in habitat factors. Since the pine and oak

TABLE 2. FOREST, ZONAL, SWAMP, AND TRUE MARSH COMMUNITIES IN TRANSECTS

Transect	Average percent salt	Forest	Shrub	Cane	Salt grass	Swamp	True Marsh
		Average level of the water table in inches					
		—30 to —4	—10 to —6	—6 to +1	—1 to +1	—4 to +12	+1 to +12
Raceland	0.0					Taxodium —Nyssa	Typha —Scirpus
Slidell	0.1 to 0.4	Pinus				Taxodium —Nyssa	Mariscus
Bayou Villars	0.3 to 1.0	Quercus		Phragmites —*Spartina cynosuroides*		Taxodium —Nyssa	Spartina —Distichlis —Juncus
Oak Island	0.1 to 1.1	Quercus	Baccharis —Iva	Phragmites —*Spartina cynosuroides*	Distichlis		Spartina —Distichlis —Juncus
Foster	1.1 to 1.5			Phragmites —*Spartina cynosuroides*	Distichlis		Spartina —Distichlis —Juncus
Yellow House	1.4 to 3.7		Baccharis —Iva	Phragmites —*Spartina cynosuroides*	Distichlis		*Spartina alterniflora*
Popich	4.0 to 4.5			*Avicennia	Distichlis		*Spartina alterniflora*

*Avicennia, although a shrub here occupies a niche similar to that filled by the canes in other transects.

forests are not closely allied to the marshes only brief mention is given them here. But since the cypress-gum swamps frequently border directly on the marshes and are subject to similar edaphic influences they are granted rather complete discussion. In addition to the vegetational units in the transects there were five aquatic communities in fresh water areas and two others in brackish water regions.

RACELAND TRANSECT

The Raceland transect extends across a cypress-gum swamp (Taxodium-Nyssa associes), a forest border of willow and buttonbush and a fresh water marsh (Typha-Scirpus associes). Water stands almost continuously on the entire transect, the average depth in the cypress-gum swamp being nearly 8 inches, that in the marsh more than 11 inches, while in the intervening willow-shrub zone it averages nearly 12 inches in depth. The cypress-gum swamp has been cut over and is somewhat open but it includes a considerable number of large trees of bald cypress *(Taxodium distichum)* and tupelo gum *(Nyssa aquatica)* and excellent reproduction of bald cypress. Of the other trees water ash *(Fraxinus profunda)* and swamp maple *(Rufacer Drummondii)* are most abundant, with black willow *(Salix nigra)* restricted largely to the swamp border. Since the swamp is rather open there is an abundance of herbaceous species some of which are found also in the marsh (Table 3). The forest border, although including many of the cypress-gum swamp species, is characterized by a greater number of willows and buttonbushes *(Cephalanthus occidentalis)*, by an abundance of cut-grass

TABLE 3. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES (SCALE 1 TO 10) IN THE CYPRESS-GUM SWAMPS (TAXODIUM-NYSSA ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Raceland (0.0 percent salt)	Slidell (0.4 percent salt)	Villars (0.6 percent salt)
TREES				
**Fraxinus profunda*	Water ash	4	....	6
Liquidambar Styraciflua	Red gum	0.1	....	....
**Nyssa aquatica*	Tupelo gum	3	....	....
**Nyssa biflora*	Sour gum	....	4	....
**Rufacer Drummondii*	Swamp maple	2	2	3
Salix nigra	Black willow	1	1	3
Tamala pubescens	Red bay	....	....	1
**Taxodium distichum*	Bald cypress	8	8	10
SHRUBS AND VINES				
Amorpha fruticosa	False indigo	....	0.1	....
Ampelopsis arborea	Pepper-vine	0.5	....	1
**Baccharis halimifolia*	Buckbrush	....	3	8
Berchemia scandens	Supplejack	0.5	....	....
Brunnichia cirrhosa	Florida-vine	1	....	4
**Cephalanthus occidentalis*	Buttonbush	4	1	2
Cerothamnus ceriferus	Wax myrtle	....	2	3
Convolvulus repens	Marsh bindweed	....	0.5	2
Ipomoea sagittata	Marsh morning-glory	....	....	2
Iva frutescens	Marsh elder	....	3	1
Mikania scandens	Hemp-vine	2	....	....
Rubus louisianicus	Swamp blackberry	1	....	....
**Sabal minor*	Dwarf palmetto	....	2	8
Sambucus canadensis	Elderberry	0.5	....	....
Styrax grandifolia	Storax	0.1	....	....
HERBS				
Achyranthes philoxeroides	Marsh-button	....	3	....
Acnida cuspidata	Southern water-hemp	....	....	2
Ageratum conyzoides	Ageratum	0.1	....	....
Asplenium ebenoides	Scott's spleenwort	0.1	....	....
Aster exilis	Slim aster	....	0.1	....
Blechnum serrulatum	Swamp fern	0.1	....	....
Bramia Monnieri	Hedge-hyssop	....	8	2
Carex comosa	Bristly sedge	0.5	....	....
Carex crus-corvi	Crowfoot sedge	1	....	....
Carex lupulina	Hop sedge	1	....	1
Chaetochloa geniculata	Marsh fox-tail	....	0.5	....
Chaetochloa magna	Giant fox-tail	....	....	0.1
Crinum americanum	String-lily	....	6	....
Cyperus virens	Swamp sedge	1	....	....
Dryopteris patens	Shield fern	0.5	....	....
Dryopteris thelypteris	Marsh shield fern	0.5	....	....
Echinochloa Walteri	Duck millet	....	0.1	2
Echinodorus radicans	Creeping bur-head	0.5	....	1
Eleocharis albida	White spike-rush	....	....	1
Eleocharis olivacea	Green spike-rush	....	0.5	....
Erianthus saccharoides	Plume grass	1	....	....
Globifera umbrosa	Dwarf moneywort	....	3	....
Gratiola virginiana	Clammy hedge-hyssop	....	3	....
Hibiscus lasiocarpus	Rose-mallow	....	1	3
Hygrophila lacustris	Water-willow	1	....	....
Hymenocallis rotatum	Spider-lily	....	4	....
Ibidium cernuum	Ladies'-tresses	0.1	....	....
Iris virginica	Coastal plain iris	....	3	....
Isnardia palustris	Marsh purslane	0.5	8	1
Juncus effusus	Common rush	....	....	5
Justicia lanceolata	Water-willow	3	....	....
Kosteletzkya virginica	Salt-marsh mallow	....	2	4
Ludwigia glandulosa	Ludwigia	1	....	....

TABLE 3 (Continued).

SPECIES	Common Name	Raceland (0.0 percent	Slidell (0.4 percent salt)	Villars (0.6 percent salt)
HERBS (Cont.)				
Myriophyllum pinnatum	Water-milfoil	....	3	....
Onoclea sensibilis	Sensitive fern	1	....	....
Osmunda regalis	Royal fern	1	1	....
Panicum anceps	Beaked panic-grass	....	1	....
Panicum agrostoides	Red-top panic-grass	....	....	2
Panicum gymnocarpon	Swamp panic-grass	2	....	2
Panicum virgatum	Feather grass	....	2	....
Persicaria Opelousana	Smartweed	3	....	....
Persicaria portoricensis	Giant knotweed	4	....	....
**Persicaria punctata*	Dotted smartweed	3	1	3
Pluchea camphorata	Spicy marsh fleabane	....	1	0.5
Pluchea foetida	Viscid marsh fleabane	....	1	....
Pontederia cordata	Pickerel weed	2	2	6
Proserpinaca pectinata	Mermaid-weed	....	0.5	....
Rumex verticillatus	Swamp dock	1	1	2
Rynchospora corniculata	Horned rush	2	....	1
Sabbatia campanulata	Slender marsh pink	....	1	....
Sacciolepis striata	Gibbous panic-grass	....	0.5	....
**Sagittaria lancifolia*	Delta potato	1	2	4
Samolus floribundus	Brookweed	....	2	1
Saururus cernuus	Lizard's tail	1	....	4
Scirpus californicus	Giant bulrush	....	....	0.1
Sesban Emerus	Coffee bean	....	....	0.5
Solidago mexicana	Seaside goldenrod	....	1	2
Spartina patens	Couch grass	....	....	1
Tradescantia reflexa	Spiderwort	0.5	....	....
Typha angustifolia	Narrowleaf cattail	....	....	2
Typha latifolia	Broadleaf cattail	....	....	3
**Zizaniopsis miliacea*	Cut grass	2	3	4
HERBS (on logs or stumps)				
Boehmeria cylindrica	False nettle	2	....	....
Hydrocotyle verticillata	Marsh pennywort	1	0.2	1
Lycopus rubellus	Water hoarhound	4	....	....
Mosses (several species)		1	1	....
Triadenum petiolatum	St. John's-wort	2	....	....
Trisetum pennsylvanicum	False oat	1	....	....
AQUATICS				
Azolla caroliniana	Floating fern	2	....	....
Ceratophyllum submersum	Coontail	0.1	....	....
Lemna minor	Lesser duckweed	2	....	....
Piaropus crassipes	Water hyacinth	1	....	....
Riccia fluitans	Dissected liverwort	0.5	....	....
Ricciocarpus natans	Heart-shaped liverwort	0.5	....	....
Spirodela polyrhiza	Greater duckweed	1	....	1
Utricularia gibba	Humped bladderwort	....	0.1	....
Utricularia macrorhiza	Common bladderwort	0.1	3	....
Vesiculina purpurea	Purple bladderwort	....	1	....

(Zizaniopsis miliacea), and by a tangle of shrubs, vines, and large herbs. The cut-grass not only is an ever present species in open cypress-gum swamps but forms a narrow zone along the borders of dense stands and is apparently a good site indicator for this community.

The marsh proper is well-developed, uniform and extensive. The predominant species are broadleaf cattail *(Typha latifolia)*, giant bulrush *(Scirpus californicus)*, and maiden cane *(Panicum hemitomon)* (Table 4).

TABLE 4. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN FRESH WATER AND NEARLY FRESH MARSHES (TYPHA-SCIRPUS ASSOCIES AND MARISCUS CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Raceland (0.0 percent salt)	Slidell (0.4 percent± salt)
Hibiscus lasiocarpus	Rose-mallow	....	1
Homalocenchrus oryzoides	Rice cut grass	3	..
Jussiaea grandiflora	Primrose-willow	0.5	..
**Mariscus jamaicensis*	Saw-grass	....	10
**Panicum hemitomon*	Maiden-cane	6	..
Phragmites communis	Roseau	2	..
Pontederia cordata	Pickerel-weed	2	..
Sagittaria lancifolia	Delta potato	1	4
**Scirpus californicus*	Giant bulrush	10	6
**Typha angustifolia*	Narrowleaf cattail	1	5
**Typha latifolia*	Broadleaf cattail	10	4
Zizaniopsis miliacea	Cut grass	2	1
AQUATICS			
Azolla caroliniana	Floating fern	0.5	..
**Castalia odorata*	White water-lily	1	2
Ceratophyllum submersum	Coontail	3	..
Lemna minor	Lesser duckweed	1	..
Limnobium Spongia	Frog's-bit	0.5	..
Myriophyllum proserpinacoides	Whorled water-milfoil	0.5	..
Piaropus crassipes	Water hyacinth	2	..
Riccia fluitans	Dissected liverwort	8	..
Spirodela polyrhiza	Greater Duckweed	1	..
Utricularia gibba	Humped bladderwort	1	..
Utricularia macrorhiza	Common bladderwort	1	1

Of the three species the latter is somewhat less abundant here and may be scarce or absent in certain portions of the community. Cut-grass and roseau *(Phragmites communis)* occur as clumps throughout the associes but are of minor importance. Since the ground surface is usually covered with water (ave. 11.2 inches) there are several submerged and floating plants in the marsh proper. Of these species the coontail (*Ceratophyllum* sp.), duckweeds *(Lemma minor* and *Spirodela polyrhiza)* floating fern *(Azolla caroliniana)* and water hyacinth *(Piaropus crassipes)* are the most abundant (Table 4).

The open water of the fresh water habitat is often coated with duckweeds and the water fern and in some ponds with introduced water cabbage *(Pistia stratiotes)*. In many lagoons the deeper portions are occupied by a submerged community of coontail (*Ceratophyllum* spp.) and/or bladderwort (*Utricularia* spp.) whereas the shallower parts are invaded by cow-lily *(Nymphaea advena)* or white water-lily *(Castalia odorata)*. Among the most important aquatics is the beautiful, but pestilential, floating water hyacinth which sometimes packs an entire lagoon or chokes a bayou to a point where navigation is quite impossible. In certain areas the water milfoil *(Myriophyllum proserpinacoides)* joins with the water hyacinth in the free-floating community. A shore-attached creeping associes of the marsh button *(Achyranthes philoxeroides)* the primrose willow *(Jussiaea grandiflora)* is usually to be found along the shores of lagoons or bayous. In some cases these species completely overrun lagoons, ditches, and bayous with the con-

sequent destruction of all other aquatics, even including the vigorous water hyacinth.

The invasion of the marsh by the cypress-gum swamp is impeded by the occasional marsh fires which are decidedly unfavorable to the ecesis of trees. But the evidence points to a slow encroachment of the swamp trees into the marsh. The forest edge, composed mostly of willow and buttonbush, contains numbers of young bald cypress, water ash, and swamp maple trees. And there are many willow and buttonbush plants as well as young seedlings

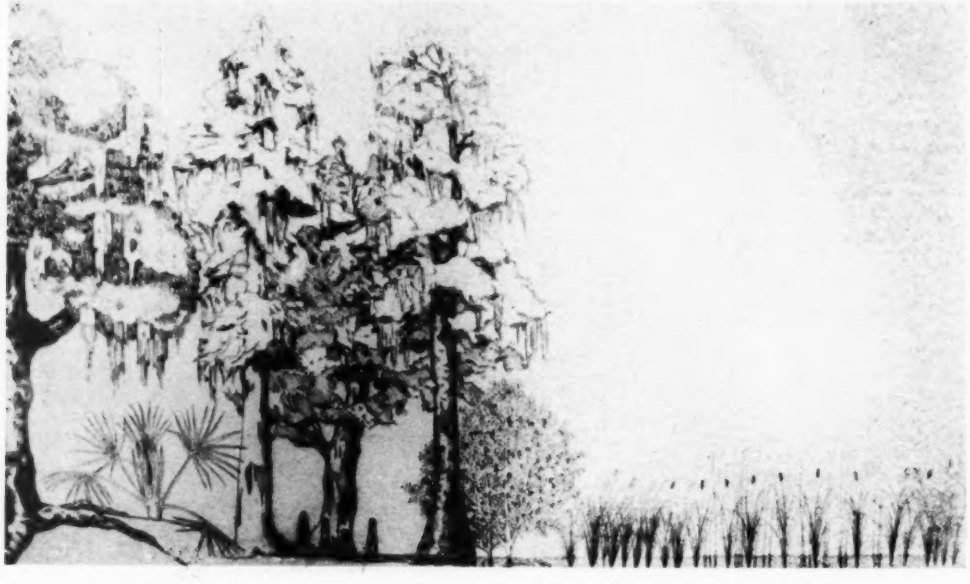

FIG. 5. Fresh water transect showing oak forest, cypress-gum swamp, and fresh water mash (left to right).

of the above species in the marsh border. However, the average depth of the water in the forest border (11.7 inches) is greater than that of the marsh (11.2 inches). Since the first foot of marsh soil contains much more organic matter (30.6 percent) than that of the forest edge (18.2 percent) the greater depth of the water is probably due to a sinking of the soil level because of the decay of this organic matter. With this unexpected difference in water level explained the evidence all points to a succession towards the cypress-gum swamp.

SLIDELL TRANSECT

In the Slidell transect examples of loblolly pine forest (Pinus consocies), cypress-gum swamp (Taxodium-Nyssa associes), saw-grass marsh (Mariscus consocies), and a water-lily community (Castalia consocies) are all represented (Fig. 6). In addition there is a suggestion of the live oak *(Quercus virginiana)* forest on the lower edge of the pine forest as well as a poorly developed shrub zone on the marsh edge of the swamp forest. All these com-

FIG. 6. Slidell transect showing pine forest, cypress-gum swamp, saw-grass marsh (background, left to right) and water-lily lagoon (left foreground).

munities occur in the short distance of 40 feet, within which the decrease in elevation is about 17 inches—a sharp slope for South Louisiana. This transect is located in a nearly fresh (faintly brackish) area. Throughout the period of study only slight traces of salt were found in the surface water, but it seems probable that during violent storms which occasionally visit this region brackish water may invade the transect. The presence in the lower edge of the pine forest of salt up to 0.5 percent in the soil water is presumably due, at least in part, to such invasions.

The pine community is characterized by an even-aged, uniform, mature stand of loblolly pine *(Pinus taeda)* and considerable reproduction of loblolly pine and red gum *(Liquidambar styraciflua)*. On the front toward the marsh the soil level declines gradually to a point near the cypress-gum swamp where it dips rather steeply. Along the lower border of the pine forest couch grass *(Spartina patens)* and black rush *(Juncus Roemerianus)* are abundant, although they occur nowhere else in the area. These two plants are typically brackish marsh species, and their occurrence only in the edge of the pine lands might seem to be anomalous, since the average salinity of the soil water in the lower pine forest was 0.3 percent, as compared with 0.4 percent in the cypress zone. These figures, however, are probably misleading. The cypress zone was covered with water during the major portion of the year, so that soil water could be obtained only during three of the driest summer months. Data from the lower pine forest taken during comparable months show a salinity of 0.5 percent. It is probable, therefore, that the

soil water of the lower pine forest actually has a higher average salinity than that of the cypress swamp, so this factor may well account for the interesting distribution of these species.

The cypress-gum swamp fringes the pine forest in a belt about 15 feet wide. It includes only four trees of which bald cypress and swamp black gum *(Nyssa biflora)* account for at least 80 percent of the stand (Table 3). Although the average salinity of the soil water is only 0.4 percent tupelo gum, water hyacinth, and many other fresh water species are excluded. Several herbaceous species such as *Crinum americanum, Iris virginica, Myriophyllum pinnatum,* and *Proserpinaca pectinata,* were found in no other cypress-gum swamp studied. This is apparently due to the acid nature of the Coastal Plain soil upon which these communities are developed.

The nearly fresh (faintly brackish) marsh (Fig. 7) is characterized by a pure stand of saw-grass *(Mariscus jamaicensis)*. Associated with saw-

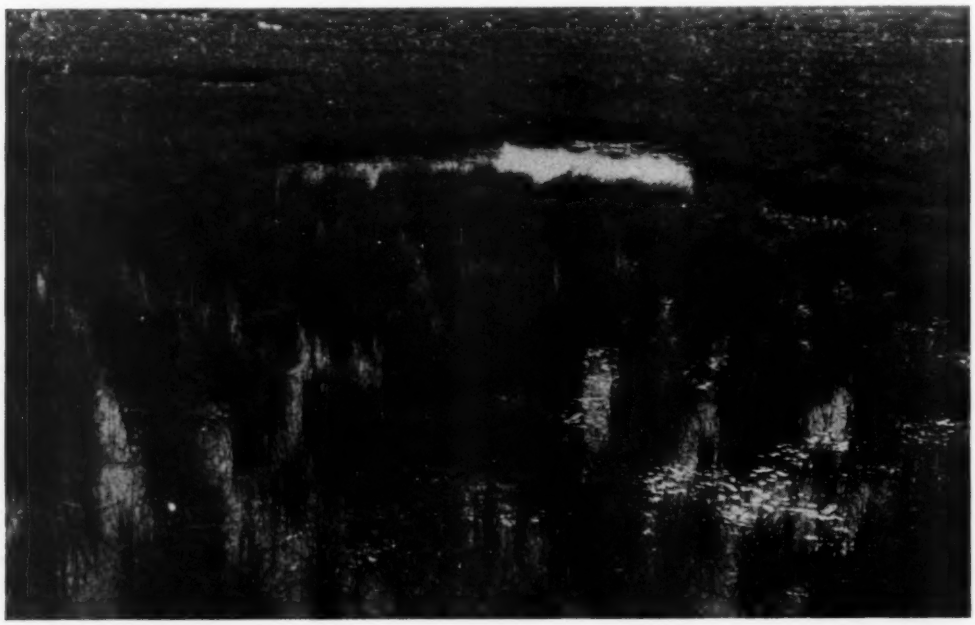

FIG. 7. Bird's-eye view of the saw-grass marsh (Mariscus consocies) showing numerous lagoons with water-lily pads.

grass, especially in deeper water, are broadleaf cattail, the narrowleaf cattail *(Typha angustifolia),* and giant bulrush (Table 4). Since saw-grass is a large aggressive species it excludes most other plants and accounts for over 60 percent of the marsh vegetation. It is probable that saw-grass, water-lily, and bladderwort constitute over 95 percent of the total vegetation. Because of this dominance the marsh is noted for a striking paucity of species. Including the lagoons, in which the only aquatic species are the bladderwort and the white water-lily, there are less than 10 species in the marsh proper.

The succession in the lagoons of this area is initiated by a submerged stage of bladderwort *(Utricularia macrohiza)*, although white water-lily *(Castalia odorata)* is usually associated with it, especially in relatively shallow water. This is often followed by an early reed-marsh stage of narrow-leaf cattail and giant bulrush, which often fringe the water-lily lagoons.

TABLE 5. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE SHRUB ZONES (BACCHARIS-IVA ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Oak Island (0.5 percent salt)	Yellow House (1.4 percent salt)
SHRUBS AND VINES			
**Baccharis halimifolia*	Buckbrush	4	10
Convolvulus repens	Marsh bindweed	0.1	1
Cuscuta spp. (on Iva)	Dodder	3	..
Ilex vomitoria	Yaupon	0.5	..
Ipomoea sagittata	Marsh morning-glory	2	2
**Iva frutescens*	Marsh elder	10	8
Rubus louisianicus	Swamp blackberry	1	..
**Sabal minor*	Dwarf palmetto	4	..
Sesban Emerus	Coffee bean	0.1	..
Smilax Bona-Nox	Bristly greenbrier	0.5	..
Vigna repens	Wild cowpea	1	..
HERBS			
Aster exilis	Slim aster	1	..
Bramia Monnieri	Hedge-hyssop	0.5	..
Carex lupulina	Hop sedge	....	1
Eleocharis albida	White spike-rush	0.5	..
Fimbristylis castanea	Sand rush	0.1	..
Hydrocotyle verticillata	Marsh pennywort	0.1	..
Iris giganticaerulea	Giant blue iris	2	..
**Panicum virgatum*	Feather grass	1	2
Phragmites communis	Roseau	0.5	1
Ptilimnium capillaceum	Mock bishop-weed	2	..
Rumex verticillatus	Swamp dock	2	..
Sacciolepis striata	Gibbous panic-grass	0.5	..
Solidago mexicana	Seaside goldenrod	3	..
**Spartina patens*	Couch grass	10	4
Vicia ludoviciana	Louisiana vetch	....	1

although saw-grass may invade directly (Fig. 13). In the marsh saw-grass usually gains the upper hand but is shaded out along the swamp border and yields to the omnipresent cut-grass. It is evident that the cypress-gum swamp is invading the marsh only very slowly since the trees are scraggly and reproducing poorly. This is probably due in part to the salt in the soil water and also to the considerable depth of the marsh water (11.8 inches). The succession in this area apparently ends in loblolly pine forest, but there are numbers of red gum, live oak, and water oak *(Quercus nigra)* trees throughout the forest as well as numerous seedlings of the same trees. In other similar forests protected for longer periods from fire the broadleaved trees are gaining at the expense of the conifers. These facts lead us to believe that this forest is subclimax and that it would be replaced by the live oak forest if protected from fire over longer periods of time.

BAYOU VILLARS TRANSECT

The authors were especially interested in the transect at Bayou Villars since this was the only area where the cypress swamp bordered a distinctly brackish marsh. This transect is nearly one-half-mile long and extends across a low section of the oak forest (Quercus association), a considerable portion of cypress-gum swamp (Taxodium-Nyssa associes), a good sample of brackish marsh (Spartina-Distichlis-Juncus associes) and a cane zone (Phragmites-*Spartina cynosuroides* associes) on the low ridge along Bayou

TABLE 6. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE CANE ZONE (PHRAGMITES-SPARTINA CYNOSUROIDES ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Bayou Villars (0.5 percent salt)	Oak Island (0.9 percent salt)	Foster (1.2 percent salt)	Yellow House (1.6 percent salt)
Achyranthes philoxeroides	Marsh button	3	..	2	...
Acnida cuspidata	Southern water-hemp	...	..	0.5	...
Aster tenuifolius	Salt marsh aster	...	..	1	1
Baccharis halimifolia	Buckbrush	1	..	1	...
Carex lupulina	Hop sedge	4	..	3	1
Chaetochloa magna	Giant foxtail	...	..	0.1	...
Convolvulus repens	Marsh bindweed	...	3	2	2
Distichlis spicata	Salt grass	...	3	...	1
Hibiscus lasiocarpus	Rose-mallow	1	..	...	...
Hydrocotyle verticillata	Marsh pennywort	...	..	0.5	...
Ipomoea sagittata	Marsh morning-glory	...	..	2	0.5
Iva frutescens	Marsh elder	...	..	1	...
Kosteletzkya virginica	Salt-marsh mallow	...	1	0.1	...
Lythrum lineare	Marsh loosestrife	...	..	1	...
**Panicum virgatum*	Feather grass	...	3	2	4
**Phragmites communis*	Roseau	10	..	3	..
Rumex verticillatus	Swamp dock	...	1	1	...
Sabbatia campanulata	Marsh pink	..	1	...	...
Samolus floribundus	Brookweed	...	..	2	...
Scirpus robustus	Three-cornered rush	...	..	...	1
Scirpus californicus	Giant bulrush	0.5	..	...	...
Senecio glabellus	Butterweed	1	..	0.5	...
Solidago mexicana	Seaside goldenrod	2	2	...	...
**Spartina cynosuroides*	Quill cane	...	10	10	10
**Spartina patens*	Couch grass	...	4	..	4
Vigna repens	Wild cowpea	...	1	...	...

Villars (Table 2). In the portion of the oak forest studied the level drops less than a foot to the cypress-gum swamp which is, in turn, about 6 inches higher than the marsh. As the bayou is approached the land rises again about 2 inches to the cane zone on the bayou bank. The water of Bayou Villars is usually almost fresh, the highest salinity noted being 0.1 percent, but the salinity of the soil water in the transect was distinctly higher. The lowest average soil salinity (0.3 percent) was found in the oak forest and about twice that amount was present in the cypress-gum swamp and cane zone. The highest salinity (1.1 percent), represented by a single determination in July, was in the marsh proper. Since soil water could be obtained here only during the dry weather of July, this figure is doubtless somewhat above the yearly average.

TABLE 7. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE SALT GRASS COMMUNITY (DISTICHLIS CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Foster (1.5 percent salt)	Yellow House (3.6 percent salt)	Popich (4.0 percent salt)
Aster tenuifolius	Salt-marsh aster	1	....	....
Avicennia nitida seedlings	Honey mangrove	....	....	2
Baccharis halimifolia	Buckbrush	0.5	....	....
Borrichia frutescens	Sea ox-eye	....	2	2
Chaetochloa geniculata	Marsh fox-tail	1	....	....
**Distichlis spicata*	Salt grass	10	10	10
Fimbristylis castanea	Sand rush	3	....	....
Iva frutescens	Marsh elder	1	....	....
Juncus Roemerianus	Black rush	1	0.5	3
Panicum virgatum	Feather grass	1	....	....
Pluchea camphorata	Spicy fleabane	2	....	....
Scirpus robustus	Three-cornered rush	2	2	....
Solidago mexicana	Seaside goldenrod	2	....	....
Spartina alterniflora	Salt cane	....	2	2
Spartina cynosuroides	Quill cane	4	....	....
Spartina patens	Couch grass	0.5	3	....

The oak forest includes considerable numbers of live oak, water oak, red gum, and hackberry *(Celtis mississippiensis)*, although the body of the forest comprises live oak and red gum as the predominant trees. In the cypress-gum swamp the elevation very gradually decreases to the marsh. The upper portion of the swamp is characterized by considerable numbers of water ash, swamp maple, and black willow. These are all eliminated toward the middle of the swamp and the only tree companion of bald cypress in the lower half of the swamp is red bay *(Tamala pubescens)* (Table 3). Cypress is progressively more dwarfed and scraggly as the marsh is approached, especially in the relatively broad swamp-marsh ecotone. This is apparently due to the higher salinity of the soil water in the marshward portion of the swamp. Since the cypress-gum swamp is very open there is a considerable herbaceous population varying from typically fresh water species *(Echinodorus radicans, Persicaria punctata, Rynchospora corniculata,* and *Saururus cernuus)* in the upper portion of this swamp to brackish water species near the marsh border (Table 3).

Of all the marshes studied the one at Bayou Villars is at once the most most cosmopolitan and the most productive of species (Table 8). It possesses not only many species which are predominant in the fresh water marshes (for example, *Juncus effusus, Scirpus californicus,* and *Typha latifolia*) but also several which are exclusively found in brackish marshes (*Aster tenuifolius, Fimbristylis castanea, Scirpus Olneyi,* and *Spartina patens*) (Table 8). Of these species couch grass is by far the most frequent and abundant and probably constitutes over 50 percent of the total marsh vegetation. Furthermore it is in this transect that couch grass attains its greatest size. It should be noted that neither salt grass, nor black rush, which are the usual associates of couch grass, is to be found in this marsh.

As is true for other stands of this community the cane zone comprises very few species (Table 6). This is due to the large size and vitality of roseau, which constitutes at least 90 percent of the mass of vegetation. In more brackish areas quill cane *(Spartina cynosuroides)* is a codominant but is practically absent here.

TABLE 8. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE BRACKISH MARSHES (SPARTINA-DISTICHLIS-JUNCUS ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Bayou Villars (1.1 percent salt)	Oak Island (1.1 percent salt)	Foster (1.1 percent salt)
Achyranthes philoxeroides	Marsh button	2	....	....
Acnida cuspidata	Southern water-hemp	1	1	0.5
Ammannia coccinea	Scarlet tooth-cup	0.1	....	....
Ammannia Koehnei	Tooth-cup	0.1	....	....
Aster exilis	Slim aster	1	0.5	....
Aster subulatus	Salt-marsh aster	....	0.5	....
Aster tenuifolius	Salt-marsh aster	1	0.5	1
Bramia Monnieri	Hedge-hyssop	2	0.5	....
Chaetochloa geniculata	Marsh foxtail	0.1	0.5	1
Convolvulus repens	Marsh bindweed	0.5	0.1	....
Cyperus Nuttallii	Nuttall's cyperus	....	0.5	....
**Distichlis spicata*	Salt grass	....	6	6
Echinochloa Walteri	Wild duck millet	2	1	....
Eleocharis albida	White spike-rush	1	....	1
Eleocharis microcarpa	Marsh spike-rush	....	1	....
Eleocharis nodulosa	Marsh spike-rush	1	..	....
Eleocharis parvula	Dwarf spike-rush	....	....	1
Eleocharis retroflexa	Dwarf spike-rush	....	1	....
Fimbristylis castanea	Sand rush	3	2	1
Hibiscus lasiocarpus	Rose-mallow	1	....	....
Hydrocotyle verticillata	Marsh pennywort	0.1	....	....
Juncus effusus	Common rush	0.5	....	....
**Juncus Roemerianus*	Black rush	....	3	6
Jussiaea decurrens	Primrose-willow	0.1	....	....
Kosteletskya virginica	False rose-mallow	0.1	0.5	1
Leptochloa fascicularis	Slender grass	1	....	....
Lythrum lineare	Marsh loosestrife	2	2	1
Paspalum vaginatum	Joint grass	3	1	....
Phragmites communis	Roseau	0.1	....	....
Phyla nodiflora	Fog-fruit	2	0.5	....
Pluchea camphorata	Spicy fleabane	....	....	1
Rumex verticillatus	Swamp dock	1	....	0.1
Sabbatia campanulata	Marsh pink	....	0.5	....
Sagittaria lancifolia	Delta potato	2	....	....
Samolus floribundus	Brookweed	1	....	....
Scirpus californicus	Giant bulrush	1	....	....
Scirpus Olneyi	Bayonet rush	2	2	2
Scirpus robustus	Three-cornered rush	....	2	....
Scirpus validus	Blue bulrush	1	....	....
Sesban Emerus	Coffee bean	0.1	....	....
Spartina alterniflora	Salt cane	....	1	1
**Spartina patens*	Couch grass	10	10	3
Typha angustifolia	Narrowleaf cattail	4	1	1
Typha latifolia	Broadleaf cattail	1	....	....
Verbesina alba	Verbesina	2	....	....
Vigna repens	Wild cowpea	1	....	....
AQUATICS				
**Ruppia maritima* (Lagoons)	Tassel-pondweed	....	....	10

TABLE 9. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE SALINE MARSHES (SPARTINA ALTERNIFLORA CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Yellow House (3.4 percent salt)	Popich (4 percent ± salt)
Distichlis spicata	Salt grass	2	2
**Juncus Roemerianus*	Black rush	10	1
**Spartina alterniflora*	Salt cane	10	10
Spartina patens	Couch grass	1	..

TABLE 10. RELATIVE ABUNDANCE OF SPECIES IN THE HONEY MANGROVE COMMUNITY (AVICENNIA CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Popich (4.5 percent salt)
**Avicennia nitida*	Honey mangrove	10
Batis maritima	Glasswort	2
Distichlis spicata	Salt grass	2
Spartina alterniflora	Salt cane	1

Apparently the cane zone is encroaching on the marsh, since young roseau occurs abundantly along the marsh border. Several facts seem to indicate, however, that the marsh grasses are invading the cypress swamp. In the first place, there is a virtual absence of seedlings and young trees of bald cypress except near the oak forest, whereas the older cypress trees are unhealthy in appearance. Moreover, "ghost forests" of dead cypress trees occur in the vicinity of the transect and many bald cypress stumps and logs largely or wholly covered by couch grass are found throughout the marsh near the swamp. Incursions of salt water from Barataria Bay which occur during heavy storms from the south undoubtedly kill and injure both seedlings and trees. In recent years these incursions have been facilitated by canalization in the area south of the transect, so it seems probable that the intervention of man has reversed the normal trend of succession and is enabling the marsh to push back the cypress swamp.

OAK ISLAND TRANSECT

Oak Island is a *chênière* situated in a brackish marsh and fringed by typical zonal communities. The transect, located on the northwestern rim of the *chênière,* includes portions of the live oak forest, the shrub belt (Baccharis-Iva associes), cane zone (Phragmites-*Spartina cynosuroides* associes), and the brackish marsh (Spartina-Distichlis-Juncus associes), but lacks the salt grass community (*Distichlis* consocies), which is present only on the southern forest border (Figs. 8, 9). This station presents more contour than most of the transects studied; the fall from the forest to the shrub zone is at least 14 inches, that from the shrub to the cane about 6 inches, and that from the cane to the marsh proper about 2 inches. On the south side of the ridge the land slopes very gradually to the marsh, but to the north it dips so steeply that all of the communities occur within the short distance of 30

feet. The lagoon at the lower end of this transect communicates indirectly with Lake Pontchartrain at times of high water, and has an average salinity of only 0.2 percent, showing almost no salt in late winter, but reaching 0.7 percent during the dry weather of midsummer. The soil water of the transect is, on the average, much more strongly brackish, the percentage of salt in-

FIG. 8. Brackish water transect showing oak forest, shrub, cane, salt grass, and brackish marsh communities (left to right).

FIG. 9. Oak Island transect showing brackish marsh (foreground), cane, shrub, and oak forest communities (left to right in background).

creasing steadily from the highest to the lowest communities (oak forest, 0.1 percent; shrub zone, 0.5 percent; cane zone, 0.9 percent; marsh proper, 1.1 percent).

The dominants of the live oak forest (Quercus association) are live oak and red gum, although several other tree species including six oaks are represented. This forest, the most prolific in species of all those studied, comprises nearly 30 shrubs and vines and over 60 herbaceous species. It is probable that the great number of species in this forest is due, at least in part, to human influence. On the southeastern margin the trees have been killed, probably by salt water, and the area is rapidly revegetating. Since the trees are too small and scattered to provide continuous shade the herbaceous population is almost wholly different from that of the forest proper.

The soil water here is too brackish for the growth of cypress and its associates but shrub and cane communities fringe the live oak forest in zones about 10 feet wide. In the shrub belt marsh elder *(Iva frutescens)* is most abundant although buckbrush *(Baccharis halimifolia)* and dwarf palmetto *(Sabal minor)* together about equal it in numbers (Table 5). Of the herbaceous components the versatile couch grass is predominant but marsh bindweed *(Convolvulus repens)*, marsh morning-glory *(Ipomoea sagittata)*, feather grass *(Panicum virgatum)* and seaside goldenrod *(Solidago mexicana)*, all characteristic of most shrub and cane communities, are well represented.

The cane zone occurs here where the average water table is near the soil surface (—0.9 inches). The important dominant is the agressive quill cane, although the smaller feather grass is abundant (Table 6). There is also a notable incursion of true marsh species, especially of couch grass and salt grass.

The brackish marsh is less cosmopolitan and much more uniform than that at Bayou Villars. This marsh, stretching away for miles with but little break in its greenish-brown cover, is among those labeled the "dreary marshes" by the writers of fiction. This uniformity is due to the fact that couch grass and salt grass, as the two major dominants, are similar in appearance and that the other principal species are not sufficiently different from these to lend much color or variety to the marsh physiognomy (Fig. 9). There are no large fresh water species here as at Bayou Villars but there are several new brackish and saline species in their stead. This marsh type is perhaps the most widespread of all and is important economically as the habitat *par excellence* of the Louisiana muskrat.

No submerged stages have been observed in the lagoons of this marsh area, although they are usually present in similar habitats elsewhere. Around the borders of lagoons the pioneer species are salt cane *(Spartina alterniflora)* and three-cornered rush *(Scirpus robustus)*. The pioneer species are followed by the dominants of the marsh proper which build up a thick substratum (1-3

feet deep) of peaty humus. The average amount of organic matter (based on the dry weight of the soil) is 55.0 percent in the first foot and 47.4 percent in the second foot of soil (Table 11). It might be assumed that the marsh in time would be succeeded by the cane belt and this successively by the shrub and forest communities as is suggested in Figure 14, but organic matter decomposes as it is elevated above the influence of salt water. The evidence, therefore, suggests that the succession here is conditioned primarily by the elevation of the marsh land by wind- and water-borne inorganic detritus and not by organic matter. In this process, of course, the plants play an important rôle in decreasing currents and otherwise contributing to the deposition of these sediments.

FOSTER TRANSECT

The most saline of the brackish stations is the Foster transect which is situated on Grand Bayou, a stream that is nearly fresh at its source but strongly saline near its mouth. Although the Foster area is somewhat more brackish than the one at Oak Island the zonal and marsh communities include the same species, although in different proportions. The transect, from the bayou front, extends across cane, salt grass, and marsh communities (Table 2). No shrub zone is included in the transect although some ex-

TABLE 11. AVERAGE EDAPHIC CONDITIONS IN MARSHES AND ADJACENT COMMUNITIES

	Water level[1] (*inches*)	Percent of salt in soil water[1]	Water content (percent of dry weight)[2]	Organic matter[2] Percent
RACELAND TRANSECT (Strictly fresh)				
Cypress-gum swamp	+ 7.8 (9)	0.0 (6)	139	16
			104	15
Forest border	+11.7 (9)	0.0 (4)	168	18
			142	11
Marsh	+11.2 (9)	0.0 (4)	207	31
			99	16
SLIDELL TRANSECT (Nearly fresh)				
Pine forest	—24.1 (9)	0.3 (8)	30	7
			27	5
Cypress-gum swamp	+ 2.5 (9)	0.4 (3)	77	21
			39	13
Marsh	+12.0 (6)	.....	354	38
			254	29
BAYOU VILLARS TRANSECT (Slightly brackish)				
Oak forest	—23.6 (7)	0.3 (7)	33	6
			32	6
Cypress-gum swamp	— 5.4 (7)	0.6 (5)	68	16
			37	6
Marsh	+ 2.5 (6)	1.13 (1)	218	37
			109	17
Cane zone	— 4.1 (7)	0.5 (5)	167	23
			114	17

TABLE 11. (Continued).

	Water level[1] (*inches*)	Percent of salt water[1]	Water content (percent of dry weight)[2]	Organic matter[2] Percent
OAK ISLAND TRANSECT (Moderately brackish)				
Oak forest	—29.8 (11)	0.1 (9)	25	6
			28	5
Shrub zone	— 6.6 (12)	0.5 (11)	46	9
			35	8
Cane zone	+ 0.7 (12)	0.9 (6)	195	29
			135	29
Marsh	+ 2.1 (12)	1.1 (5)	475	55
			452	47
FOSTER TRANSECT (Strongly brackish)				
Cane zone	— 4.7 (9)	1.2 (9)	178	25
			154	19
Salt grass	— 1.0 (9)	1.5 (6)	592	46
			316	18
Marsh	— 0.6 (9)	1.1 (6)	729	57
			389	45
YELLOW HOUSE TRANSECT (Saline)				
Shrub zone	— 9.8 (10)	1.4 (10)	57	10
			82	8
Cane zone	— 5.4 (10)	1.6 (10)	113	13
			111	8
Salt grass	— 0.4 (10)	3.7 (8)	154	17
			148	17
Marsh	+ 0.7 (10)	3.4 (3)	259	24
			273	23
POPICH TRANSECT (Strongly saline)				
Honey mangrove	— 2.2 (10)	4.5 (9)	106	9
			118	11
Salt grass zone	+ 1.3 (10)	4.0 (3)	110	10
			150	11
Marsh	+ 2.3 (10)	not determined	142	10
			163	14

[1] Under "Water level" the + and — signs indicate levels above and below the soil surface. The number of determinations of water level and salinity on which each of the averages is based is indicated in parenthesis.
[2] Under "Water content" and "Organic matter" the two figures given refer to the first and second feet of soil, respectively. Each of these figures is an average of 2 to 4 determinations.

amples occur in the region. The difference in ground level between the highest and lowest parts of the transect is only about 4.5 inches, since the cane zone averages 3 inches higher than the salt grass zone which, in turn, is about 1.5 inches higher than the marsh proper. As regards salinity of soil water, the three plant communities are remarkably similar, the average salinity in the cane zone being 1.2 percent; in the salt grass zone, 1.5 percent; in the marsh, 1.4 percent.

In the cane zone (Phragmites-*Spartina cynosuroides* associes) quill cane is the major dominant although roseau and feather grass are represented as minor codominants (Table 6). The cane community here is similar to that in the Oak Island transect except that it embraces a greater number of

species. Since the average water table is lower here (—4.7 inches) than at Oak Island, where it is very close to the soil surface, the cane zone includes fewer marsh species and none of the true marsh dominants.

The salt grass belt (Distichlis consocies) is a distinctive community characterized by the relatively small and attractive salt grass. This species forms practically a continuous stand, although scattered plants of many species appear throughout the community. The sea ox-eye *(Borrichia frutescens)* which is the most common associate of the salt grass elsewhere, is not found here (Table 7).

The brackish marsh (Spartina-Distichlis-Juncus associes) in the Foster transect is of more than passing interest since it represents the last stand of the couch grass under increasingly saline conditions (Fig. 10). Of the dom-

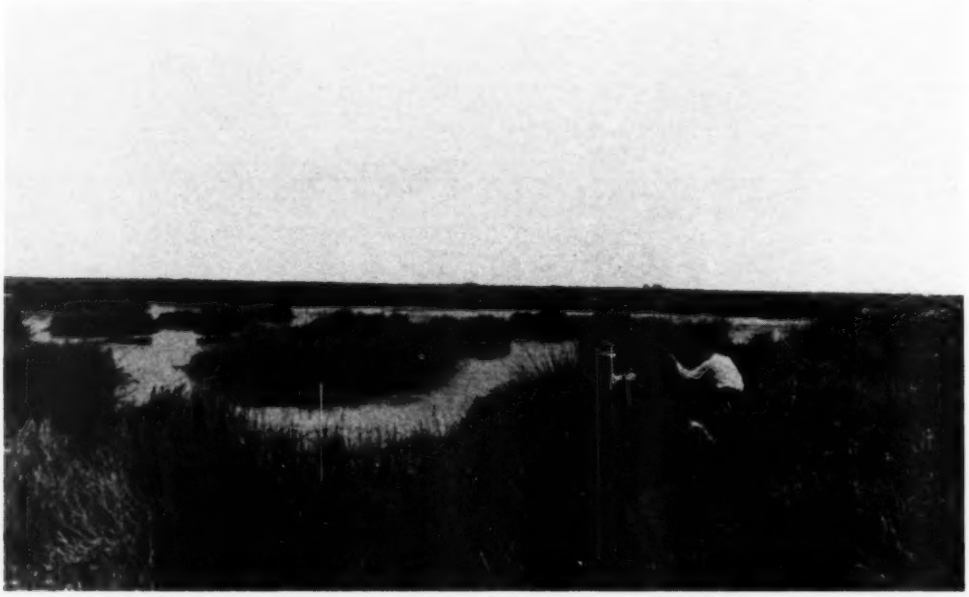

FIG. 10. Brackish marsh (Spartina-Distichlis-Juncus associes) at the Foster transect.

inants salt grass and black rush are about equal in numbers but couch grass is much less abundant (Table 8). Of the other components bayonet rush *(Scirpus Olneyi)* and the spike rushes *(Eleocharis albida* and *E. parvula)* are numerous near muskrat houses, probably due to the creation of relatively bare areas by muskrat activity. In addition four species, common to higher communities, were found growing on abandoned, decomposing muskrat mounds. In this marsh the organic content of the soil was higher than in any other. This has led to the conclusion that peaty humus accumulates most rapidly where the salinity is low enough to permit excellent plant development and yet sufficiently high to prevent rapid decay. These conditions obtain in the marsh of the Foster area.

The lagoons become choked with the tassel pondweed *(Ruppia maritima)* into which the marsh dominants soon enter (Fig. 13). However, ditches are invaded by salt cane which usually forms a pure stand. These habitats are not readily entered by the marsh dominants since considerable elevation must be accomplished before they can survive. It is probable that the salt grass zone is encroaching on the marsh since there is vigorous reproduction of salt grass in the border zone, but there is little evidence that the cane zone is infringing on the salt grass community.

YELLOW HOUSE TRANSECT

The topography along the bayou front here is very different from that in any other transect. It is the practice of fishermen to dump old oyster shells in the shallow water along the shore of the bayou. Here a ridge of partially decomposed shells is covered by about 10 inches of clayey mud which also fills the interstices between the shells. In addition a fore-land of fine sediments about 8 feet wide and about 3 inches lower than the ridge has been laid down on the bayou side. The transect, from the bayou edge, extends across a salt grass community, a shrub zone on the crest of the ridge and, at successively lower elevations, cane, salt grass, and true marsh communities. Since the two salt grass zones are similar except for a greater abundance of sea ox-eye in the bayou front community, only the innermost is listed in Table 7. From the highest to the lowest community the average ground level falls about 9 inches in 100 yards, the slope from shrub zone to cane being 4 inches, from cane to salt grass, 4 inches, from salt grass to marsh, 1 inch. Striking variations in salinity of soil water are noted at the different levels, as indicated by the yearly averages in the four communities: shrub zone, 1.4 percent; cane zone, 1.6 percent; salt grass zone, 3.6 percent; marsh, 3.5 percent.

The shrub belt (Baccharis-Iva associes), because of its comparatively low salinity, supports several species that are relatively intolerant of salt, among which are buckbrush and roseau. Of the dominants buckbrush is more abundant than marsh elder. As is usual in shrub zones marsh bindweed, marsh morning-glory and couch grass are present, the latter in considerable abundance. It will be noted, however, that the number of species represented is much lower than that in the Oak Island transect (Table 5).

The cane community (Phragmites-*Spartina cynosuroides* associes) is similar to the one at Foster but includes less than half as many species. Of the dominants quill cane, considerably outnumbers both roseau and feather grass. The salt grass zone (Distichlis consocies) comprises only five species, two of which, black rush and salt cane, are dominants of the marsh proper. Of the other three species, sea ox-eye and couch grass are common but salt grass constitutes over half of the total vegetation in the community (Table 7). It is of interest that couch grass, the main dominant of brackish marshes,

is here more abundant in every zonal community than it is in the marsh proper.

Couch grass and salt grass which are major dominants of brackish marshes, are very rare in the saline marsh (*Spartina alterniflora* consocies). The major dominant in the saline marsh is usually salt cane, but black rush is an important codominant in this area. This is a marsh with high salinity, moderate organic matter (24.3 percent) and a paucity of both plant and animal species. Nevertheless this marsh is of great importance in reclaiming shallow lagoons and mud banks throughout the saline areas bordering the Gulf, the successional stages being very similar to those in the Foster area.

POPICH TRANSECT

The Popich transect is unique in that it includes a total of only six plant species, among them the remarkable honey mangrove *(Avicennia nitida)*. The transect cuts across a wide zone of honey mangrove, a band of salt cane, a narrow belt of salt grass and ends in the low salt cane marsh (Fig. 11). This zonation differs from the typical pattern of the area in the presence of the band of salt cane next to the mangrove. It is difficult to account for this band of salt cane since its elevation is even greater than that of the salt grass community. In any case the salt grass zone is usually adjacent to the honey mangrove whereas the salt cane is usually found at lower elevations.

The crest of the bayou "ridge," occupied by the mangrove zone, stands 3 inches above the main body of the marsh, and was never seen under

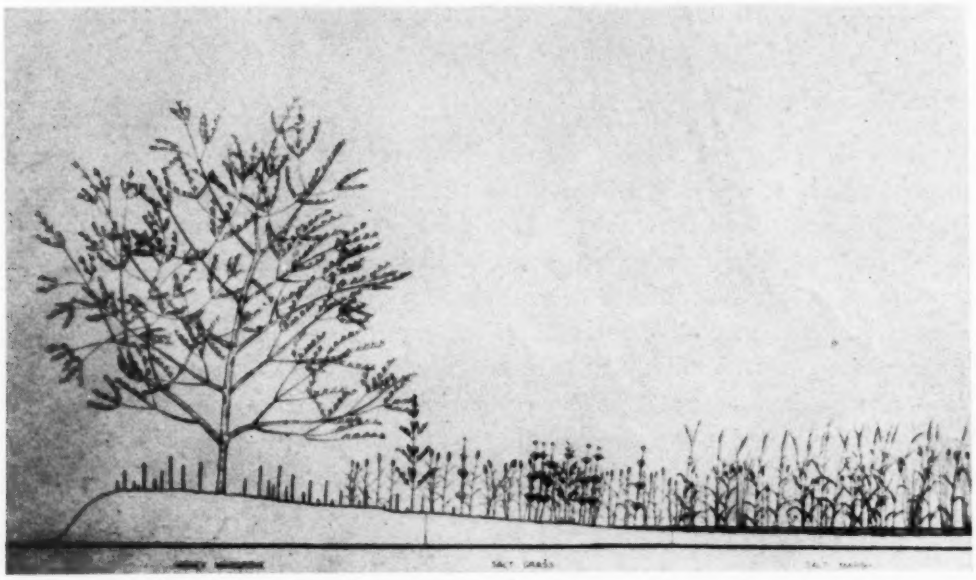

FIG. 11. Saline transect showing honey mangrove, salt grass, and saline marsh communities (left to right).

water except at times of strong onshore winds. In the outer salt cane belt (2 inches lower than the mangrove) the water level is typically just above or just below the soil surface, and the same is true of the salt grass zone which is one-half-inch still lower. A further drop of about an inch marks the transition to the marsh proper, which was never seen without standing water. Salinity in the bayou (varying with season and weather from 0.9 to 3.2 percent) averaged 2.3 percent, and in the surface water of the marsh it

FIG. 12. Popich transect showing honey mangrove and marsh communities (left to right).

averaged nearly the same. The soil waters, however, were more strongly saline (mangrove zone, 4.5 percent; outer salt cane zone 3.7 percent; salt grass zone, 4.0 percent). No soil water determinations were obtained from the marsh proper because of the continual presence of surface water.

Without doubt the honey mangrove zone (Avicennia consocies) is the most striking of all the marsh communities (Fig. 12). It is characterized by a dense stand of honey mangrove with a scattering of glasswort *(Batis maritima)* (Table 10). Honey mangrove is an evergreen shrub, up to 25 feet in height, characterized especially by terete, aerenchymous root knees about 16 inches high. These knees are probably of value in gaseous exchange although the average water table is 3 inches below the soil surface. Since honey mangrove readily invades the lower communities and would occupy a much larger area except for annual marsh fires, the "knees" are probably of real service in ecesis in the wetter habitats. In addition the soil is covered by storm tides several times in the course of a year. The fruit of honey mangrove, including one seed with two peculiarly folded cotyledons is shed in

December. When the soil surface is covered with water in the winter and early spring these fruits germinate as they float about over the various marsh communities. When the water recedes the hairy radicles take root and seedlings develop. Since the salinity of the surface water is usually less than 1 percent in the winter whereas that of the soil is around 4 percent this method is considered as a means of survival since the seeds are said not to germinate readily in a medium of high salinity (Joshi, 1933).

The salt grass zone (Distichlis consocies) closely resembles the stands of this community found elsewhere. Salt grass forms an almost continuous stand in which occur scattered plants of its common associate, sea ox-eye (*Borrichia frutescens*). The only other species found here are black rush, salt cane, and seedlings of honey mangrove (Table 7). These mangrove seedlings occur mainly in the upper edge of the zone, whereas salt cane is somewhat more abundant in the lower portions; otherwise the species named are about equally frequent throughout the community.

The saline marsh (*Spartina alterniflora* consocies) presents a nearly pure stand of the salt cane (Table 9). The plants of this species are notably dwarfed, and they blend, in general appearance, with the much less abundant salt grass, so that only the occasional patches of black rush serve to break the monotony of the great stretches of this dreary marsh. The upper two feet of soil in this marsh are well filled with rhizomes and roots, providing a fairly solid substratum; but, though some roots continue to a depth of 5 feet, the soil is so mucky and fluid that a 3-inch auger may easily be pushed from the 18-inch to the 5-foot level with one finger. The organic content of the soil is relatively low (10.3 percent for the first foot of soil and 14.4 percent for the second foot). Presumably this is due to the fact that the plant structures decompose very slowly while silt is being deposited rather rapidly, every storm from the South submerging the area in water and depositing a film of sediment. The importance of salt cane in stabilizing these deposits is obvious.

The deeper lagoons of this marsh are usually free of plants, except for a few algae, but salt cane readily invades the shallower portions, and as the marsh is being built up, the higher communities are definitely advancing over the lower (Fig. 13). This is particularly evident in the case of honey mangrove. Not only is there a gradation in size of mangrove away from the bayou, but there is abundant migration of its seedlings into the grass communities. Furthermore, there is a considerable mass of partially decomposed rhizomes and roots of marsh species even under the densest stand of honey mangrove.

GENERAL NOTES ON VEGETATION

In the preceding descriptions the areas studied have been classified, on the basis of salinity, into two major habitat groups, the *fresh water* and the *salt water* habitats. The fresh water habitats include not only the *strictly fresh*

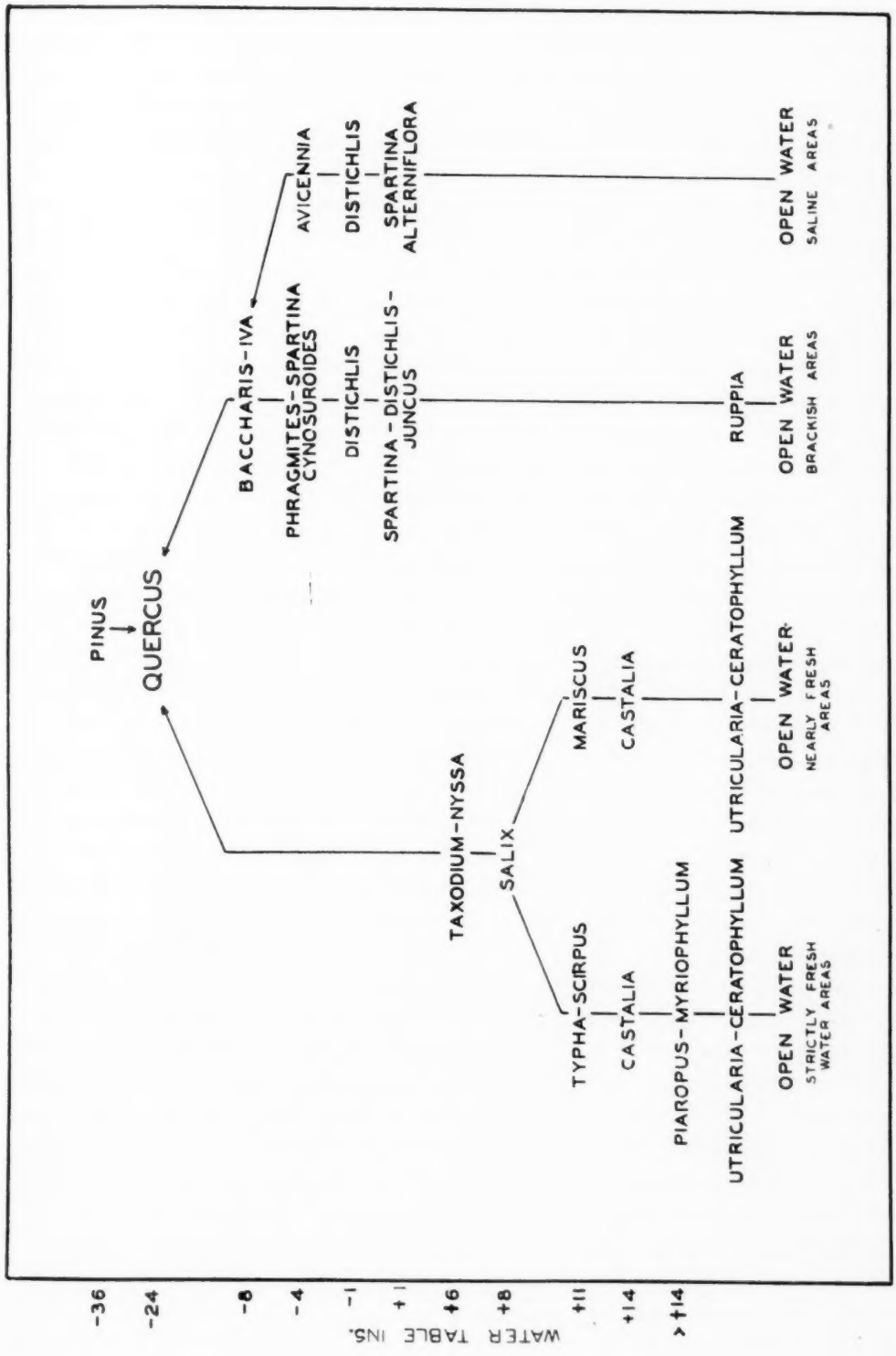

FIG. 13. Chart showing the probable successional relations of the plant communities of the marsh habitats.

water areas, but also the *nearly fresh* (faintly brackish) areas, in which the average salinity of the soil water does not exceed 0.5 percent. The *brackish* areas which have salinities of 0.5 to 2.0 percent and the *saline* areas in which the average salinity range is from 2.0 to 5.0 percent have been included as salt water habitats. The reasons for making the diversion at this point will become apparent later.

In the fresh water habitats the elevations in the marshes, if high enough, support pine or oak forest which is replaced, at lower levels, by cypress-gum swamp and marsh. As observed by the writers the pattern is always the same —pine or oak forest, cypress-gum swamp, marsh. The outstanding feature of these marshes is the presence of sedges or grasses 8 to 12 feet tall. Two distinct marsh associes are recognized in these areas. The *strictly fresh water* marsh is populated by broadleaf cattail and giant bulrush, whereas the *nearly fresh* (faintly brackish) marsh is given over largely to saw grass. In addition the nearly fresh water areas include several species typical of salt water marshes but only in the lower zonal communities where there is an appreciable amount of salt in the soil water.

In salt water habitats the vegetation pattern is quite different. Cypress-gum swamp is absent, and pine or oak forest is flanked, at successively lower levels, by zones of shrub, cane, and salt grass, beyond which lies the marsh whose dominant species, low in stature (2 to 4 feet), are in striking contrast with the towering species of the fresh water marshes. Since the shrub, cane, and salt grass communities form belts around the forest they are referred to as *zonal communities*. Our evidence seems to indicate that the transition from 0.4 percent to 0.6 percent in the average salinity of the soil water is responsible for the elimination of the cypress-gum swamp and the appearance of the zonal communities.

The zonal communities of shrub, cane, and salt grass present several points of interest. Like the cypress-gum swamp of the fresh water areas, they stand between the oak forest and the marsh, but whereas the cypress is typically found in permanent standing water, these zonal communities are usually present where the average water level is one or more inches below the surface. Among these communities the shrub belt stands out in bold relief because of the size and evergreen character of the dominant species. The cane zone, although occurring at a slightly lower elevation than the shrub belt, is also conspicuous, since it occupies a much greater area than the shrub community and is composed of very large grasses from 8 to 16 feet high. The salt grass belt is not conspicuous because of the small size of the predominant species. Near the coast it is often partially or wholly replaced by a conspicuous evergreen community of honey mangrove. The zonal communities usually fringe the rivers and bayous; hence the traveler in the marshlands, whether going by boat or by highways built on the bayou banks, is apt to gain the impression that these communities are very impor-

tant components of the marshland vegetation. However, from various survey trips we have estimated that they occupy less than 5 percent of the total marshland area.

The shrub zone is poorly developed in fresh water areas, but it is usually well developed in brackish habitats wherever the soil level is high enough. On the other hand the cane zone or salt grass or both may be entirely absent. The cane zone is usually absent in the most saline habitats (Popich transect, Grand Isle, Louisiana, and Cat Island, Mississippi) whereas salt grass is lacking in slightly brackish habitats (Bayou Villars and Oak Island transects). Of the dominants in the cane zone roseau is rare in highly brackish habitats and even quill cane is eliminated in the saline habitats in the immediate vicinity of the Gulf. Instead the salt grass zone is bordered at higher elevations by a shrub zone in which marsh elder and sea ox-eye are the important shrubby components.

In salt water habitats the low ground of the paludal basins is occupied by a typically extensive marsh in which water from one to a few inches deep typically stands on the surface through most of the year. The writers have recognized two marsh communities in the salt water area—the brackish marsh (Spartina-Distichlis-Juncus associes) and the saline marsh (*Spartina alterniflora* consocies). The brackish marsh may be represented by pure stands of couch grass in slightly brackish areas or by pure stands of black rush in sandy areas but there is usually an admixture of one or both of these species with salt grass. Of the three dominants couch grass is the least tolerant of salt and, therefore, is replaced by the other two in strongly saline areas. Since both black rush and salt grass have wide ranges of salt tolerance which overlap with that of salt cane, the dominant of the saline marsh, the brackish marsh merges insensibly into the saline marsh. These facts emphasize the difficulty of delineating these marsh communities and indicate that the present nomenclature must be regarded as tentative.

Several cases of peculiar distribution of species should be mentioned here. Cut-grass is most abundant on the marshward fringes of the cypress-gum swamp-forest and is usually a good site indicator for this forest. In addition it is very abundant in young marshy areas which young cypress trees are invading. It may even occur in nearly pure stands over a considerable area in which case it approximates a true marsh community, but it is never of importance in well developed marshes. It appears, therefore, that it often forms a marsh-like seral stage but is replaced later either by mature marsh or the cypress-gum swamp. The two tall "canes", *Phragmites communis* and *Spartina cynosuroides*, typically occur in a cane zone where the average water level was found 3.4 inches below the soil surface. However, in relatively fresh water areas they occur where the average water level is near or even above the soil surface and may even approximate the status of true marsh dominants. This is true in many localities near Lakes Borgne and

Pontchartrain and near the mouth of the Mississippi River. *Distichlis spicata* is a versatile species which not only occurs in nearly pure stands in the salt grass zone throughout the salt water habitats but it is a very wide-ranging marsh dominant from slightly brackish to very saline conditions. *Juncus Roemerianus* is an important marsh dominant in the brackish and saline marshes but attains its maximum abundance and size in sandy areas where it constitutes what Mohr calls the "black rush formation."

The successional relations in the marsh habitats are not known with certainty, but from the juxtaposition of communities, and especially from their relations to the average water levels, some idea of the probable course of succession may be deduced (Fig. 13). Doubtless there is considerable deviation from this typical pattern, especially in regard to the successions leading to the marsh, shown in the two lines at the left in Figure 13. Furthermore it should be noted that no attempt has been made to suggest what the secondary successions might be. Investigations are now under way to determine these detailed successional relationships.

EDAPHIC FACTORS

Of the factors governing the composition and distribution of marsh communities it was clearly evident from the beginning that the edaphic factors were of first importance. After preliminary tests we decided to make routine determinations of the following factors in every community: (1) the water level with reference to the soil surface; (2) salinity of free soil water (or of surface water when present) and that of adjacent bayous and lagoons; (3) water content of the soil, based on dry weight; and (4) percentage of organic matter in the soil. Organic matter was tested from two to four times at each station; all other determinations were made, so far as practicable, once a month for 12 months. It was clearly recognized that certain other determinations, such as pH, dissolved oxygen, and salinity of capillary water, would have been highly desirable, but time limitations made it impossible to include them.

It is perfectly obvious that tests made once a month throughout one year do not constitute a quantitatively accurate study of fluctuating factors such as water level and salinity, but we feel that the data thus obtained do make possible a significant comparison of living conditions at the different stations. The comparisons between the communities of a given transect are believed to be fairly satisfactory since, in each case, all the zones were studied on the same day and under approximately the same conditions. The comparisons of the different transects are not quite so satisfactory because of variations in weather conditions under which the different stations were visited. Our records show, however, that a wide range of wet and dry conditions, in both winter and summer, was encountered at each transect.

SALINITY

METHODS

The study of salinity has been based mainly on free soil water. Surface water was tested also, but, except as it influences soil water, it is not believed to be of great importance in determining the distribution of plant communities, since the absorbing organs of plants are rarely in contact with surface water. Therefore, unless otherwise stated, the *salinity data for each community refer to the salinity of its free soil water.*

The method of taking samples was as follows. On each of the monthly trips to a given area surface water was collected from the transect, if present, and also from the adjacent bayou or lagoon. Soil water was collected, so far as possible, from each community by boring a hole of appropriate depth with a soil auger and allowing it to fill to approximately constant level from the surrounding soil. It will be noted (Table 11) that there is great varation in the number of soil water samples obtained in the different zones of a transect. This is due to the frequent presence of surface water in the lower communities and to the depth of the water table in the higher communities. For example, in the marsh proper at the Raceland, Slidell, and Popich transects, no soil water samples were obtained, due to the continual

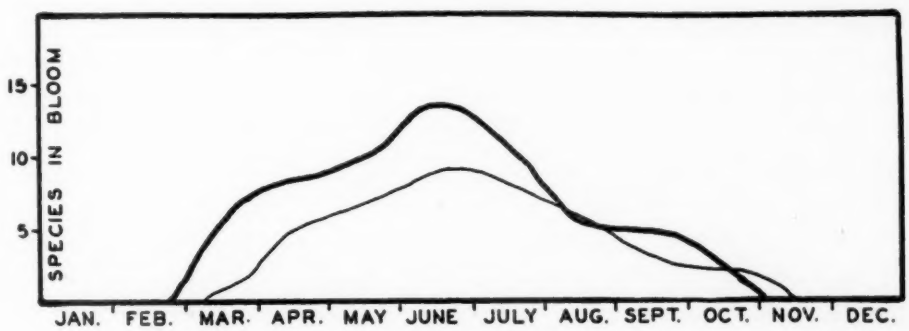

FIG. 14. Relative anthesis in the strictly fresh water marsh at Raceland and nearly fresh water marsh at Slidell (light line).

presence of surface water, and in several other communities the same condition obtained except in dry weather. On the other hand, in the forests at the Slidell and Oak Island transects, the water table could be reached with a 6-foot auger only after heavy rains.

Salinity determinations were made hydrometrically by a method which was standardized during the early stages of the work. Several of the determinations were checked by gravimetric and volumetric methods which seemed to indicate that the hydrometric determinations were accurate to within 0.1 percent of salt. A fuller discussion of the method used and factors influencing the results will be presented in a separate paper.

RESULTS

In the presentation of our findings we have dealt mainly with averages rather than with individual determinations, since the salinity at a given point fluctuates widely with season and weather. Therefore, unless otherwise indicated *each datum on salinity of either soil water or surface water is the average of the determinations made on all the monthly samples collected at a given point.* The evidence now in hand, the most important parts of which are summarized in Table 11, seems to justify the following conclusions:

1. *The salinity of surface water in the marshes does not greatly exceed that of the adjacent lagoons, bayous, and lakes.* Presumably this is due partly to the heavy rainfall and partly to the innumerable lagoons in which, at most points, frequent interchange occurs between tidal pools and the permanent open waters. At the Oak Island transect, where the surface water of the marsh and that of the lagoon are continuous after every

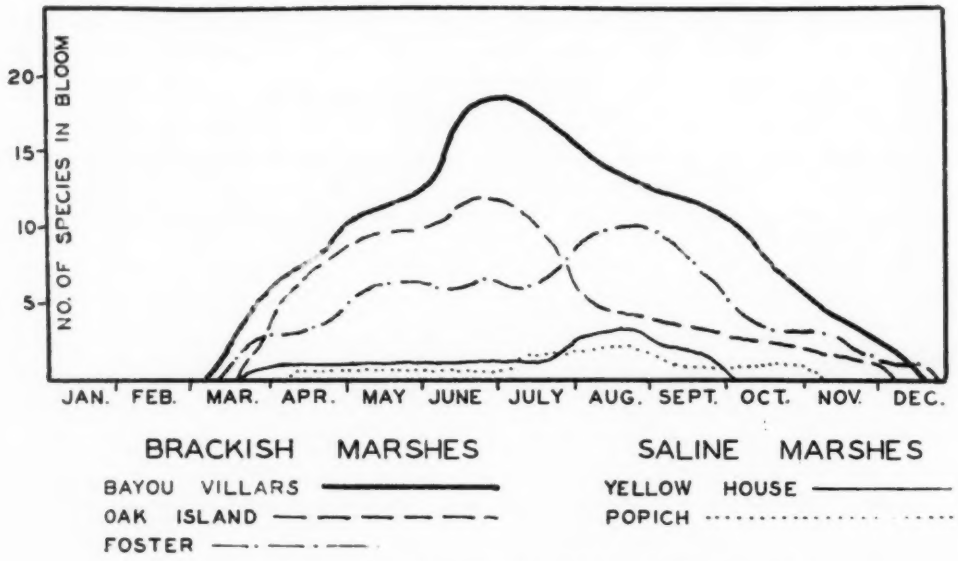

FIG. 15. Relative anthesis in the brackish and saline marshes.

heavy rain, the average salinity in both is identical (0.2 percent), but at the Yellow House transect where a bank several inches high prevents communication between bayou and marsh except at times of very high water, the salinity in the surface water of the marsh averages 2.4 percent as compared with 2.0 percent in the bayou.

2. *The free soil water in marsh communities, as a rule, is decidedly more saline than the water of nearby lagoons, bayous, and lakes.* At the Popich transect, for example, the water of Grand Bayou contained, on the average, 2.3 percent of salt while the soil water of the honey mangrove zone showed nearly twice that concentration (4.5 percent). In the nearly fresh (Slidell) transect the proportionate difference is even greater, the 0.4 percent of salt

in the soil water of the cypress-gum community being at least eight times the average amount present in the permanent standing water of the marsh. In only three of the twenty-four communities listed in Table 11 (forest at Oak Island, shrub and cane zones at Yellow House) was the soil water found to be less saline than the adjoining body of open water, and all these communities were situated 5 inches or more above the average level of the open water. Just how the relatively high salt concentrations in the soil are maintained in the presence of a 60-inch rainfall is a question of considerable interest. Obviously surface evaporation and transpiration play a part, but their relative importance is by no means clear.

3. *The highest salinity in an area is usually found in a community where the average water level is just above or just below the soil surface.* This is not surprising, since surface evaporation from saturated soils should be rapid, and leaching should be expected to be relatively ineffective at these low levels. The following comparison illustrates the principle.

Transect	*Community of highest salinity*	*Average water level in that community*
Popich	Honey mangrove (4.5 percent)	—2.0 inches
Yellow House	Salt grass (3.7 percent)	—0.4 inch
Foster	Salt grass (1.5 percent)	—1.0 inch
Oak Island	Marsh proper (1.1 percent)	+2.0 inches
Slidell	Cypress-gum (0.4 percent)	+2.5 inches

These data bring out the additional fact that, in the transition from saline to nearly fresh water areas, the zone of greatest salinity was found at progressively lower elevations. The significance of this fact is by no means clear.

4. *With progressive elevation of the soil surface more than a few inches above the water level of the bayou or lagoons there is a progressive decrease in the salinity of the soil water.* At the Yellow House transect, for example, where the marsh proper is just about at the level of the water in Grand Bayou, the salt grass zone with its high salinity of 3.7 percent is approximately 1 inch above the marsh; 4 inches higher in the cane zone the salinity drops to 1.6 percent, and another rise of 4 inches brings us into the

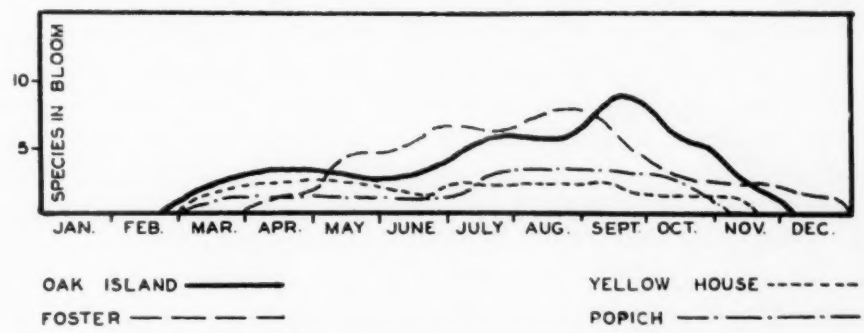

FIG. 16. Relative anthesis in the salt grass communities.

shrub zone on the crest of the bayou ridge where the salinity is only 1.4 percent. These decreases are especially noteworthy in view of the large size and high evaporating power of the shrub and cane communities whose plants, 8 and 10 feet tall, are in striking contrast with the scarcely knee-high salt grass.

5. *The marsh types in Southeastern Louisiana are closely correlated with salinity.* The stricty fresh-water marsh (Typha-Scirpus associes) is found in areas where the hydrometer shows no trace of salt. The saw grass marsh (Mariscus consocies) occurs where the salinity is less than 0.5 percent. Although no soil water samples were obtained in the saw grass marsh at the Slidell transect this conclusion is supported by the determinations made in the other communities at that transect and also by data obtained from other stands of the saw grass community. The average salinity of the brackish marsh (Spartina-Distichilis-Juncus associes) varies from 0.5 to 2.0 percent, and that of the saline marsh (*Spartina alterniflora* consocies) ranges from 2.0 to 5.0 percent (Fig. 17). Since every plant has its own range of salt tolerance there is a gradual transition from the nearly fresh to the saline marsh type, with broad ecotones, often several square miles in extent, connecting them.

WATER LEVEL

Anyone who wades the marshes of South Louisiana may readily observe that the water in salt water marshes is not as deep as it is in fresh water marshes. In saline areas the vegetation does not usually invade deep water, a depth of 4 inches or more being found only in open lagoons, whereas, in fresh water areas, a tall marsh vegetation commonly stands in water a foot or more deep. More careful study shows that, in the transition from brackish to fresh water conditions, both zonal and marsh communities are found growing at progressively lower elevations. Four examples of this principle may be cited. Quill cane dominates the cane zone in 3 of the transects studied. At Yellow House (salinity 1.6 percent) it is 5.4 inches above the water table; at Foster (1.2 percent salt) it is 4.7 inches above water table; but at Oak Island (0.9 percent salt) water averaging nearly an inch in depth covers the cane zone. The same general relations are shown by the shrub zone, the cypress-gum swamp, and the brackish marsh (Table 11).

All these observations are closely related to certain facts discussed in the section on salinity. For example, in the saline Yellow House area, the shrub and cane communities have established themselves only on the higher ground where salinity is much less than in the marsh proper, but at stations farther inland, where the zone of greatest salinity occurs at lower levels, the shrub and cane communities are found thriving at progressively lower elevations.

The relations of salt grass to water level are quite different from those just described, for, in going from saline toward fresh water habitats, it is found at progressively *greater* elevations. At the Popich transect (4.0 per-

cent salt) it is covered by more than an inch of water; at Yellow House (3.7 percent salt) it is nearly half an inch above the water table; and at Foster (salinity 1.5 percent) it is 1 inch above average water level.

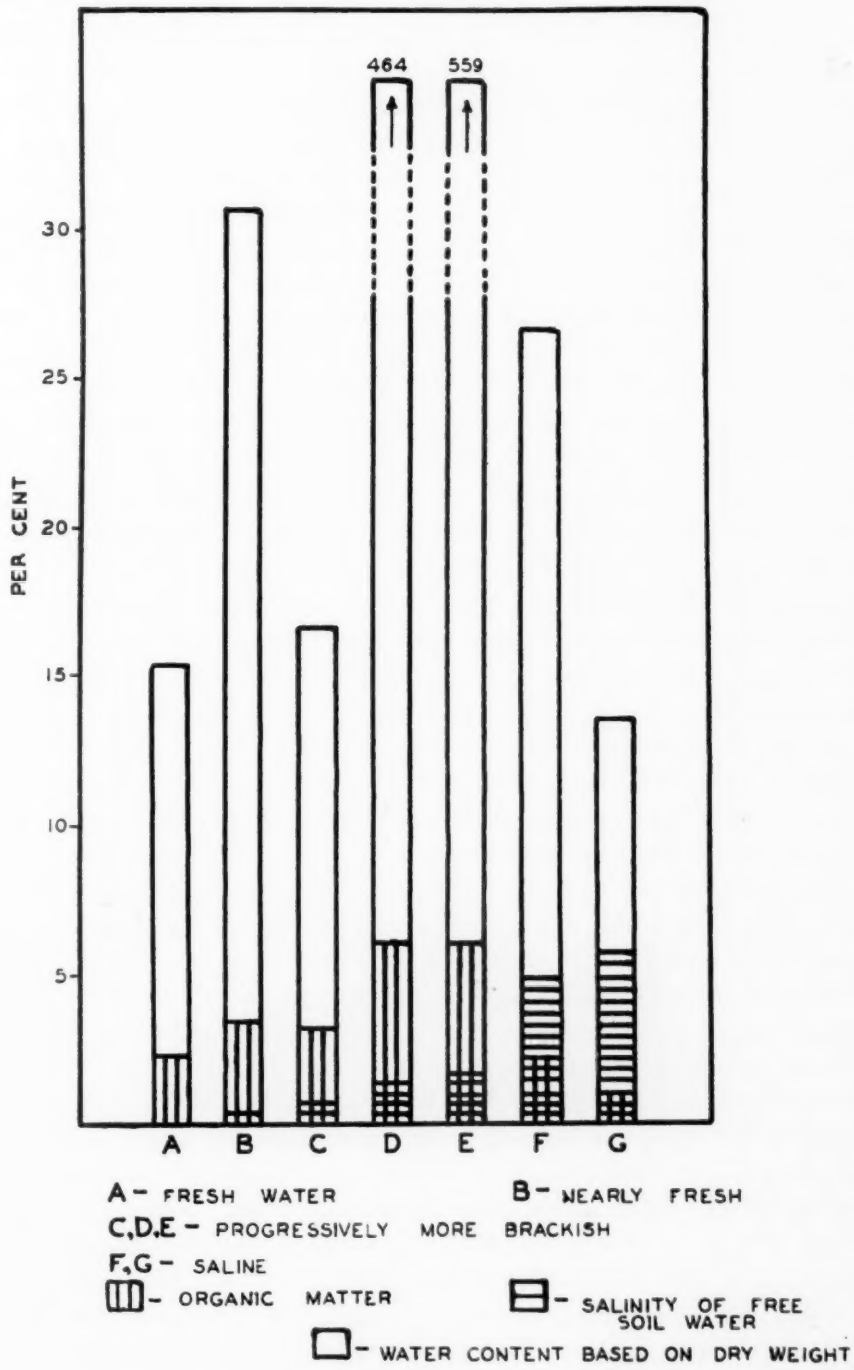

FIG. 17. Average edaphic conditions in the true marshes.

The reason for this reversal of relationships is not fully understood, but apparently salt grass, unlike the typical brackish water species, is favored by high salinity and normally occupies the most saline parts of every area where it grows unless crowded out by honey mangrove. In relatively fresh water areas the greater number of communities occurs where there is considerable surface water but in brackish or saline areas nearly all the communities occur where the mean water table approximates or is somewhat below the soil surface (Fig. 13). In fresh water ponds submerged, free-floating and attached floating communities are usually present but the only aquatic stage present in brackish lagoons is a submerged community and even this is absent in saline water bodies. Since the cypress-gum swamp borders directly on the marshes of fresh water areas, the shrub and cane communities, so typical of brackish areas, are absent in these habitats.

WATER CONTENT AND ORGANIC MATTER

In marsh communities the average percentage of soil water, as based on the dry weight of the soil, ranges to an astounding degree. During the period of investigation the least soil water (8.1 percent) was found in the first foot of soil of the oak forest at the Oak Island transect on July 24, 1932, and the greatest amount of water (867.1 percent) was obtained exactly one month later in the first foot of soil in the brackish marsh in the Foster transect. The average water contents of the pine and oak forests (25 to 32 percent) are not unlike those reported elsewhere, but the average in soils of marsh communities (98 to 728 percent) are striking and rarely encountered in ecological literature (Table 11). From the above figures it is evident that the water is from 0.98 to 7.28 times the weight of the solid material which constitutes the soils. In general the percentage of soil water was lowest on the *chênières* and ridges and greatest in the marsh proper. The percentage of water was thus progressively higher in the following communities: pine forest, oak forest, shrub zone, cypress-gum swamp, cane belt, salt grass zone, and marshes (Table 11).

In general, the organic content (based on dry weight) is least on the islands and ridges and progressively greater at lower elevations. The lowest percentage of organic matter (3.0 percent) was found in the first foot of soil in the pine forest of the Slidell transect and the greatest amount (59 percent) in the first foot of soil of the marsh of the Foster transect. In the marshes proper, it is relatively low in both fresh water and saline areas and progressively higher toward the brackish marshes (Fig. 17). The same sequence is true for the water content of marsh soils. Thus the average water content in the first two feet of soil is relatively low (153 percent) in the fresh water marsh, becomes progressively higher in the more brackish areas until it reaches a peak in the highly brackish marsh (559 percent) and relatively low again (142 percent) in the saline marshes (Fig. 17). The rel-

atively high water content of brackish marsh soils is undoubtedly due to the high percentage of organic matter contained therein. This in turn, is probably due to the favorable balance of plant growth over plant decomposition. In fresh water marshes growth and decomposition are rapid; in saline marshes both processes are slow; but in brackish marshes growth is excellent whereas decomposition is greatly retarded.

In soils which are rarely saturated the ratio of water content to organic matter is relatively low and fluctuating but in the soils of lower communities this ratio is high (about 10 to 1) and comparatively constant. Stated otherwise, the amount of organic matter in saturated soils is approximately 10 percent (8 to 12 percent of) that of the water content. Due to more abundant rhizomes, roots, and partially decomposed aerial parts in the first foot of soil the organic content is usually about 50 percent greater than it is in the next lower foot of soil. This relation does not obtain, however, in the saline marsh of the Popich transect (Table 11). In this marsh there was much more silt and clay in the first 6 inches of soil than in the soil below. This is undoubtedly due to frequent baths of detritus-laden water driven in by onshore winds. It is probable that the low organic content of the first foot of soil is due to the relatively greater amount of silt and clay therein. Despite the above facts there is an abundance of roots and rhizomes to a depth of 2 feet or more and numerous roots to a depth of 5 feet. This was true even under honey mangrove where no grasses whatever were present and where there probably had been none for several years.

SALT TOLERANCE

On the basis of the salinity of the soil water our swamp and marsh dominants may be arranged in four salinity groups (Table 12). The species of the first group, including two swamp and three marsh species were never found except in purely fresh water. They are the true halophobes of our region. Usually included in this group by most investigators are all those plants listed in the second group. It will be noted, however, that although they may grow in purely fresh water and may even be characteristic of fresh water marshes or swamps they do tolerate a considerable amount of salt.

There are several species of interest in the second group. Bald cypress, codominant with tupelo gum in fresh water swamps throughout the South, is accompanied by swamp maple and water ash into the slightly brackish areas but it leaves these species to venture into still more brackish water where its only woody companion is the red bay. Ghost forests of bald cypress are numerous in the Lake Pontchartrain-Lake Borgne region where this forest borders the saw grass marsh. There has been considerable speculation as to the cause of the destruction of these trees. All the available evidence points to salt water, brought inland by the historic hurricane in 1915, as the

TABLE 12. RELATIVE SALT TOLERANCE OF THE IMPORTANT SPECIES IN THE MARSH TRANSECTS STUDIED

SPECIES	Percent salt
STRICTLY FRESH WATER SPECIES	
Mikania scandens	(0.0)
Myriophyllum proserpinacoides	(0.0)
Nyssa aquatica	(0.0)
Panicum hemitomon	(0.0)
Piaropus crassipes	(0.0)
FRESH OR NEARLY FRESH WATER SPECIES	
Achyranthes philoxeroides	(0.0 — 1.48)
Castalia odorata	(0.0 — 0.2)
Cephalanthus occidentalis	(0.0 — 0.89)
Crinum americanum	(0.21 — 0.53)
Iris virginica	(0.21 — 0.53)
Mariscus jamaicensis	(0.0 — 0.2)
Nyssa biflora	(0.21 — 0.53)
Persicaria punctata	(0.0 — 0.89)
Pontederia cordata	(0.0 — 0.89)
Sagittaria lancifolia	(0.0 — 0.89)
Scirpus californicus	(0.0 — 1.13)
Taxodium distichum	(0.0 — 0.89)
Typha angustifolia	(0.0 — 1.68)
Typha latifolia	(0.0 — 1.13)
Utricularia macrorhiza	(0.0 — 0.53)
Zizaniopsis miliacea	(0.0 — 0.89)
BRACKISH WATER SPECIES	
Aster tenuifolius	(0.55 — 2.30)
Baccharis halimifolia	(0.0 — 1.98)
Borrichia frutescens	(0.87 — 4.43)
Convolvulus repens	(0.45 — 2.04)
Distichlis spicata	(0.45 — 4.97)
Fimbristylis castanea	(0.23 — 1.93)
Ipomoea sagittata	(0.23 — 2.04)
Iva frutescens	(0.21 — 1.98)
Juncus Roemerianus	(0.12 — 4.43)
Kosteletzkya virginica	(0.21 — 1.80)
Lythrum lineare	(0.55 — 1.68)
Panicum virgatum	(0.21 — 2.04)
Phragmites communis	(0.0 — 2.04)
Scirpus Olneyi	(0.55 — 1.68)
Scirpus robustus	(0.64 — 3.91)
Solidago mexicana	(0.18 — 1.93)
Spartina cynosuroides	(0.55 — 2.04)
Spartina patens	(0.12 — 3.91)
Vigna repens	(0.23 — 1.26)
SALT WATER SPECIES	
Avicennia nitida	(3.68 — 4.97)
Batis maritima	(1.33 — 4.97)
Spartina alterniflora	(0.55 — 4.97)

destructive agency. Saw-grass is usually considered a fresh water species by most investigators. The writers have never found it in other than faintly brackish areas, except as relicts in areas from which salt water has been excluded. It is usually accompanied by white water-lily and bladderwort, both of which are typical of fresh water ponds. Cut-grass is a species which inhabits shallow canals or bayous, open cypress-gum swamps or forms a fringe of varying extent along the borders of dense stands of this community. It

is an unfailing companion of bald cypress in all its habitats and apparently is a good site indicator for the cypress-gum associes.

The list of species in the third group (Table 12) includes no trees or important fresh water species but does include practically all the important brackish marsh species. Even in this group several species occur which may be found growing in purely fresh water areas. Of these, *Achyranthes philoxeroides, Baccharis halimifolia, Phragmites communis, Samolus floribundus,* and *Typha angustifolia* may be found in fresh water habitats and it is here that they attain their best development. In the less saline of the brackish marsh transects the great "wet prairie" borders directly on the cane zone but in most brackish and salt marshes a salt grass zone is interposed between the cane associes and the marsh proper. With the exception of the honey mangrove community, which often replaces salt grass, the greatest salinity of the marsh grasslands is attained in the salt grass zone (up to 4.4 percent of salt). In the brackish marshes couch grass is the dominant *par excellence.* By virtue of its considerable size (up to 5 feet), its bunch grass form, its tremendous vigor and great range of salt tolerance this species is able to drive out most of its competitors. In more saline areas its size and vigor decrease and it shares dominance with black rush and salt grass. In still more saline areas it is entirely eliminated, largely in favor of salt cane.

The last group includes the true "salts" of the marsh grasslands. Honey mangrove and glasswort, which clan together on the bayou ridges, have been found in no other marsh area. Furthermore salt cane is of little importance in any other marsh but here constitutes more than 75 percent of the total vegetation and becomes of great importance in extending the land seaward in the saline habitat.

A casual inspection of the species list (Table 12) shows that most species have a wide range of salt tolerance. The narrowest range occurs in species whose upper limit of salt tolerance is very low. From this it may be inferred that the more salt a plant tolerates the greater its probable range. A probable exception to this rule is shown by the range of honey mangrove which thrives typically only in saline areas. In general typical brackish and saline species grow readily and much larger in somewhat fresher areas. Notable examples are couch grass and salt cane. In slightly brackish marshes (Bayou Villars transect) couch grass blooms at a height of 50 to 60 inches whereas in saline habitats (Yellow House transect) it is less than 18 inches high. In brackish marshes, especially in ditches, the flowering stalks of salt cane are 60 to 80 inches high whereas in saline marshes (Popich transect) they are less than 20 inches in height. It has been observed also that under conditions of high salinity plants are larger and healthier at higher elevations and along the shores of bayous, possibly due to better aeration obtaining under such conditions. Notable for their extreme ranges in salt tolerance are couch grass, black rush, salt grass, and salt cane. These species

are all major dominants in the brackish and saline areas, and probably aggregate 75 percent of the total vegetation in these marshes.

In only one report on salinity of marsh soils (Harshberger, 1911) that the writers have seen have determinations of salinity of soil water been made. In Harshberger's work samples were taken at various times at three localities near Belmar, New Jersey, but apparently not in any definite chronological sequence. Although he gave only the hydrometer reading we have converted these into percentages of salt at 15°C. in order to compare them with our results. In converting, a probable error as great as 0.2 percent is introduced but in spite of this his results parallel ours fairly closely. *Spartina alterniflora, Spartina patens,* and *Distichlis spicata* all have a range of salinity very similar to our determinations for these species and he states that the former two are very widespread and controlling in the New Jersey marshes. With Phragmites, Baccharis, and *Aster tenuifolius* there is a general agreement but he gives *Solidago mexicana, Spartina cynosuroides, Panicum virgatum* and *Typha angustifolia* a salt tolerance of less than 0.5 percent and classes them as fresh water species.

Visits to the New Jersey marshes and our experience and data indicate that his conclusions regarding these four species are quite untenable. It is probable that these data were founded on one or a very few determinations. In any event conclusions on ranges of salinity should be attempted only after the determination of many samples for one or more years or at least during the growing period of the community under investigation.

BIOTIC FACTORS

Of the biotic factors influencing the vegetation man is the most important. Many fresh water marshes have been reclaimed to make the richest of agricultural lands. This is effected by pumping the water from a system of canals into a leveed bayou. In many cases these reclamation projects have been abandoned due to insufficient or improper financing. Since the land sinks when it is drained the original marsh reverts to an open water area one to four feet deep when the projects are abandoned. Even in brackish marshes the land may be reclaimed, usually for sugar cane or rice production, as for example near the Foster transect, where a large portion of the marsh was formerly under rice cultivation. In certain cases the drained areas have never been used for crop production. In such marshes the vegetation develops rapidly, through stages quite unlike those in the natural sere, to a more mesic type. In addition to the drainage projects there has been a tremendous development of navigation canals. These have served to promote rapid run-off and also to bring about abnormal fluctuations in water level and salinity due to storms and tidal action.

Another important influence of man on the marshes is through the medium of fire. It is the practice of muskrat trappers to fire the marshes an-

nually just prior to or during the trapping season. This is done to make walking less laborious, to find traps more readily, and to improve the muskrat food. There is some question on this last point but it is known with certainty that couch grass is adversely affected by fire and gives way largely to the three-cornered rush and bayonet rush, considered the best of the muskrat food plants. Fire, by removing the stalks of the previous year, decreases the amount of organic matter returned to the soil and thus impedes the elevation of the marshes. If the marsh is fired when the soil is wet in the absence of wind, little damage is done and a considerable fire hazard is removed. But in periods of extended drought, especially where the area is dissected by canals, the peaty humus, usually from one to three feet in thickness, becomes very inflammable and, when fired, burns furiously. This results not only in the destruction of both active and dormant plant parts, and the production of possibly injurious alkali but also in a lowering of the marsh level, and therefore, a reversion to a more hydric community in the sere.

Muskrats injure plants by feeding on their rhizomes, and in the making of burrows and houses. Around many of the houses the marsh is partially denuded for a radius of several feet and in most of these areas bayonet rush is abundant. Several mesic species, typical of higher communities but not found elsewhere in the marsh, grow on the muskrat houses. In addition, two spike-rushes (*Eleocharis* spp.), and bayonet rush, are especially abundant in areas partially denuded by muskrats. At present it is impossible to estimate the effects of muskrat activity on marsh vegetation but it would not be surprising to find that it modifies considerably the marsh composition and development. In heavily brackish areas fiddler crabs, horse mussels, and certain snails are very abundant but their effect on the vegetation is not obvious. The direct effect of the ubiquitous salt marsh mosquitoes is also of no importance but their indirect effects are far-reaching. In many areas they have impeded the ecesis of man, thereby reducing greatly the destructive activities of this major biotic factor and tending to preserve the marshes in their primeval condition.

PHENOLOGY OF THE MARSHES AND ASSOCIATED COMMUNITIES

Phenological data were obtained throughout an annual cycle by monthly trips to the seven areas under investigation. In the case of all plants the stage of development, the conditions of buds, the stage of flowering, the presence and condition of fruit, and time of dissemination of seeds were carefully observed and entered in tabular form in field notebooks. Symbols or combinations of symbols for the phenological stages were devised and monthly records were kept for each species by the aid of these symbols. It should be stated that it was often impracticable to return to the areas ex-

actly one month following previous visits. Because of this the authors are unwilling to postulate the exact periods of anthesis of particular species at any one station. It is believed, however, that the community data supplied in Figs. 14, 15, and 16 represent typical conditions for our marsh vegetation.

In Louisiana blooming plants are usually found during every month of the year. This is especially true in forest communities where certain of the trees start their anthesis in January. Certain of the species (*Pontederia cordata, Piaropus crassipes, Sagittaria lancifolia,* and *Vigna repens*), may bloom for 8 months or even more although some species have a flowering period of less than 3 weeks. Certain other species may have one blooming period in the spring and one in the autumn. Foremost among these are *Sambucus canadensis, Berchemia scandens, Cerothamnus ceriferus, Iva frutescens, Solidago mexicana, Spartina patens, Distichlis spicata, Zizaniopsis miliacea,* and *Aster tenuifolius.*

Because of the mild winters and exceptionally long growing period (326 days) the seasonal aspects do not correspond in chronology or duration to those usually indicated in textbooks of ecology. The prevernal period, comprising the month of February and the early part of March, is ushered in by the blooming of species in the shrub and cane communities. These include *Carex lupulina, Hydrocotyle verticillatus, Cerothamnus ceriferus, Rumex verticillatus,* and the conspicuous butterweed *(Senecio glabellus).* Compared to the vernal aspect, which includes most of March and the month of April, the prevernal phase is characterized by meager anthesis. More species begin flowering in the vernal aspect than during any similar period of the year. In the same aspect the anthesis of the true marsh species is inaugurated (Figs. 14, 15). Important among these are giant bulrush and maiden cane *(Panicum hemitomon)* of the fresh water marsh; and bayonet rush, black rush, and couch grass of the brackish marshes. The estival aspect (May, June, July), begins with a month of reduced activity but enough new species initiate flowering in the fresh water, nearly fresh, and moderately brackish marshes to produce a maximum number of flowering species before the end of the aspect.

Several vernal and still more estival species continue in bloom throughout August and September (autumnal aspect). A goodly number of species initiate flowering during the autumnal aspect especially in the heavily brackish and saline marshes (Fig. 16). Conspicuous during this phase are the cottony heads of buckbrush, the yellow clusters of the seaside goldenrod *(Solidago mexicana),* the nodding plumes of roseau, the strict panicles of salt cane, and the numerous blue and white heads of salt-marsh asters. A few prevernal and a progressively smaller number of estival and autumnal species continue to bloom during October and November. In the marshes alone there were sixteen species in flower during October and ten species in November. Since no new species inaugurate anthesis during these months it is deemed im-

proper to assign this period to the autumnal aspect. We are, therefore, designating these months as the postautumnal aspect. During this aspect there is a gradual deterioration of the vegetation which is hastened by progressively colder weather. The leaves of the grasses and sedges dry in place with a rapid change to tans and browns. These become the dominating colors of the marsh panorama and are broken only by the green of the buckbrush and marsh elder. Since there is little or no anthesis during December and January in true marsh communities this period is logically labelled as the hiemal aspect. But all is not inactivity; the shoots of Hydrocotyle, Rumex, Senecio, Scirpus, Sagittaria and many another plant are vegetating as early as late December and are well advanced before the prevernal aspect is introduced in February.

In the cypress-gum swamps species are in bloom throughout the year since the bald cypress initiates anthesis in late December or January and swamp maple, black willow and wax myrtle *(Cerothamnus ceriferus)* begin flowering in January. There is then no true hiemal aspect in the forest communities. In general anthesis is inaugurated first in the oak forest and progressively later in the cypress-gum swamps, shrub zones, cane communities, fresh water marshes, nearly fresh, brackish, and saline marshes. Although flowering in the above communities is initiated in the above order it is terminated in approximately the reverse sequence. Despite the fact that the general onset of anthesis is later in the more brackish areas the blooming of a given species is usually earlier the more saline the habitat.

In general more species were found to flower in spring (April-May) and early autumn (August-September) although several communities are characterized by a summer (June-July) maximum. The cypress-gum swamp, in fresh water areas, exhibits a characteristic spring (April-May) and a lesser autumn (September-October) maximum. But the cypress-gum swamp in faintly brackish habitats is characterized by a summer (June-July) peak only (Fig. 15). In the oak forest there are more woody plants in bloom in the early spring (April) than in any other aspect but in the brackish cypress-gum swamps the peak is not reached until June. Since the herbaceous population also reaches its flowering crest during June the complete graphs for the brackish swamps display notable summer maxima.

Only two examples of the shrub community (Baccharis-Iva associes) were studied. Both of these exhibited characteristic spring (April-May) and autumn (August-September) peaks. This is of interest since the more brackish community on Grand Bayou possesses only one-third as many species as the shrub zone at Oak Island. The cane community (**Phragmites-***Spartina cynosuroides* associes) usually includes few species since both of the large canes are very vigorous and readily oust their competitors. Despite this relative paucity of species they show unmistakable vernal (April) and autumnal (September) peaks. The salt grass community (Distichlis con-

socies) is well developed only in the more brackish and saline areas. It is also characterized by a scarcity of species, fourteen being the greatest number encountered in any one of these communities (Fig. 16). Of the four examples studied all exhibit an autumnal maximum in anthesis. There may be a less prominent rise in July but there are few vernal species. The marshes proper differ considerably in their phenology (Figs. 14, 15). The relatively fresh water marshes, as well as the less salty of the brackish marshes (in Bayou Villars and Oak Island transects), have the greater number of species in bloom during the estival (June-July) aspect, whereas the more brackish and saline ones are characterized by autumnal (August-September) maxima.

UTILIZATION OF THE MARSHES

Under natural conditions the marsh habitats afford a great variety and quantity of animal life of considerable value to man. The marshes include especially a great diversity of bird and aquatic life. Not only are they the home of many resident game girds but they also constitute the winter home of a majority of ducks, geese and other waterfowl which nest in North America east of the Rockies. Because of this fact the problem of the preservation of these marshes has attracted state, national, and even international attention. Perhaps the best known marsh animal is the Louisiana muskrat which thrives best in the brackish habitat. Of the aquatic life proper there is an abundance of shrimp, fish, and other organisms in the innumerable bayous, lakes, and lagoons which are present in these areas. The value of these natural resources is measured not only in the economic return but also in the incentive which they give for healthful outdoor sport, recreation, and education.

It has been estimated by Viosca (1928) that the money value of these natural resources aggregated over twenty million dollars in 1924-1925. Of the marsh animals the muskrat is the most important having contributed a product worth six and a half million dollars. The balance of the revenue came largely through the sale of shrimp, crabs, fish, oysters, frogs, turtles, and alligators. Of the plants the three-cornered rushes, which furnish the best muskrat foods, are the most important economically but some of the grasses such as couch grass and salt grass furnish pasturage for cattle which wade out into the marshes to feed. In addition couch grass is utilized in broom-making since it is green when properly cured and requires less labor than broom corn in broom manufacture. Revenue also is derived from the army of pleasure seekers and sportsmen who visit the marshes yearly and who contribute largely to the support of numerous guides and resort keepers. The Louisiana marshes still constitute a mecca for the hunter, fisherman, and nature-lover. Since the marsh areas are the home of a remarkable variety of plants, fish, frogs, and birds they serve to attract many stu-

dents and nature-lovers. In addition a number of species exist here which are used in educational institutions throughout the world.

Many of the marshes, especially in the salt water habitats, still retain their primitive status, but many of the "wet prairies" have been much modified by fire, canalization, and drainage. When the water level is lowered a few inches the land is suitable only for grazing. But when the level is lowered still further by means of a system of levees and pumps the land is fine for the production of corn, rice, and even sugar cane. There are many thousands of acres in the fresh water region west of the Mississippi that have been drained to make suitable agricultural land. A notable development is the area between Raceland and Houma. Unfortunately the heavy overhead for flood protection and drainage has caused the failure of many of these reclamation projects. Since drainage destroys valuable natural resources without producing benefits proportional to the reclamation costs it is probable that further reclamation should not be attempted in the near future in the marshes of southeastern Louisiana.

SUMMARY

1. *Scope of investigation.*
   a. This investigation deals with the composition, development and phenology of plant communities in marshland areas and with the causal factors in the distribution of the component species.
   b. The work reported in this paper extended over a period of four years. It involved 23 reconaissance trips, 66 routine studies made in seven transects during one annual cycle and about 20 confirmatory trips subsequent to the routine investigation.

2. *Areas studied.*
   a. The region is one of little relief but the streams are flanked by natural levees, which slope gradually away from the stream front to paludal basins, in which the soil surface is usually covered with water.
   b. Each transect was so established as to include all the communities on the elevations and a considerable portion of marsh proper in the paludal basin.
   c. Of the transects studied in detail one was located in a fresh water area, a second was in a nearly fresh area (less than 0.5 percent salt); three were located in brackish areas (0.5 to 2.0 percent salt) and two were in saline areas (2.0 to 5.0 percent salt).

3. *Communities in the transects.*

In the transects studied the writers recognized 11 distinct communities of which three are forests, four are zonal communities in which the average water level is below the soil surface, and four are true marshes in which water usually stands on the soil.

   a. In the strictly fresh water area (Raceland transect) an oak forest (Quercus association) is bordered at lower elevations by the cypress-gum swamp (Taxodium-Nyssa associes) in which bald cypress and

tupelo gum are the dominant species. A forest fringe in which black willow and cut-grass are the conspicuous species, separates the cypress-gum swamp from a vast marsh (Typha-Scirpus associes) in which giant bulrush and broadleaf cattail account for the bulk of the vegetation.

b. In the nearly fresh habitat (Slidell) a forest of loblolly pine is fringed on the marshward side by cypress-gum swamp (Taxodium-Nyssa associes) in which swamp black gum is substituted for tupelo gum. The cypress-gum swamp borders directly on the saw-grass marsh (Mariscus consocies) which consists mainly of saw-grass.

c. In the slightly brackish transect (Bayou Villars) the cypress-gum swamp (Taxodium-Nyssa associes) includes bald cypress as the sole dominant. Here the cypress swamp abuts directly on a brackish marsh (Spartina-Distichlis-Juncus associes) which includes one major dominant, couch grass. This marsh is the most cosmopolitan of all since it embraces both fresh and brackish water species.

d. In the moderately brackish transect (Oak Island) the oak forest is fringed at progressively lower elevations by shrub, cane, and true marsh communities. The shrub belt (Baccharis-Iva associes) is characterized by a predominance of marsh elder. The cane zone (Phragmites-*Spartina cynosuroides* associes) is distinguished by a single dominant, quill cane. The brackish marsh (Spartina-Distichlis-Juncus associes) is a uniform, extensive "wet prairie" including couch grass and salt grass as the dominant species.

e. The strongly brackish habitat (Foster transect) embraces cane, salt grass, and brackish marsh communities at gradually decreasing elevations away from the bayou. The cane zone (Phragmites-*Spartina cynosuroides* associes) comprises *Spartina cynosuroides* as the major dominant and *Phragmites communis* and *Panicum virgatum* as minor codominants. In the salt grass belt (Distichlis consocies) salt grass, Distichlis spicata, forms a nearly continuous stand. Of the species in the marsh proper (Spartina-Distichlis-Juncus associes) salt grass and black rush are the predominant species.

f. Of the two transects in saline areas, the one of lower salinity is the Yellow House transect. Here the bayou ridge, underlain by oyster shells, supports a shrub community. This is paralleled at successively lower levels by cane, salt grass and true marsh communities. The shrub, cane, and salt grass communities are not conspicuously different from those previously described except for a notable paucity of species. The saline marsh (*Spartina alterniflora* consocies), also characterized by a scarcity of species, is almost entirely composed of salt cane and black rush.

g. In the most saline habitat (Popich transect) the bayou front is populated by the unique honey mangrove, which is the sole dominant of the Avicennia consocies. This is paralleled, away from the bayou, by a salt grass zone (Distichlis consocies) in which salt grass is the predominant species. The body of the area is a saline marsh (*Spartina alterniflora* consocies) in which salt cane accounts for most of the vegetation.

4. *General vegetational relations.*

   a. The fresh water areas, including strictly fresh and nearly fresh habitats (less than 0.5 percent salt), are characterized by the presence of a cypress-gum swamp and a marsh of tall sedges and grasses from 8 to 12 feet tall. The salt water areas, including brackish and saline habitats (0.5 to 5 percent salt) are distinguished by the absence of the cypress-gum swamp, the presence of zonal communities, and a marsh of small grasses, sedges, and rushes from 2 to 4 feet in height.

   b. In the salt water habitats three zonal communities (shrub, cane, and salt grass zones) often occur on the bayou ridges above the level of the marsh proper. These four communities may be found on a slope having a fall of less than one foot. Therefore the transition from one community to another may be conditioned by a change in elevation of less than 3 inches.

   c. The dominants of the fresh water marshes include broadleaf cattail, narrowleaf cattail, giant bulrush and sawgrass. The dominants of the salt water marshes are: couch grass, black rush, salt grass and salt cane. These species account for the bulk of the marsh vegetation and constitute the great "double quartet" of the marshes of southeastern Louisiana.

5. *Edaphic factors.*

Of the habitat factors the water level and salinity of the soil water appear to be the most important, although soil moisture (and possible organic matter) may be influential locally or during unfavorable periods.

   a. Salinity.

      (1) Individual determinations of salinity fluctuate widely with season and weather; comparisons are therefore made on the basis of year-round averages.

      (2) Free soil water in marsh communities is usually more saline than the surface water of the marsh, that of adjacent lagoons, bayous, and lakes.

      (3) In a given area the highest salinity is usually found in a community where the average water level is close to the soil surface.

      (4) The higher the land level, the lower is the salinity of the soil water. (This is true for all elevations except the first few inches above the adjacent open water.)

      (5) Strikingly different types of marshes are found in strictly fresh, nearly fresh, brackish, and saline areas.

      (6) With increasing salinity, marsh dominants and several other plants are progressively stunted.

   b. Water level.

      (1) Depth of water in the marsh proper is greatest in fresh water areas; it decreases progressively with increasing salinity.

      (2) Aquatic communities are present in fresh water bodies but are lacking in salt water lagoons.

      (3) The greater the salinity, the higher is the elevation at which most species grow. (The true halophytes are exceptions.)

(4) In salt water habitats several plant communities are found where the mean water table is near or below the soil level.

c. Water content and organic matter.

(1) Water content and percentage of organic matter in the soils are lowest in the pine and oak forests, and successively higher in the shrub, cypress-gum, cane, and salt-grass communities.

(2) In the marshes proper the water content is relatively low (absolute minimum 98 percent) in the fresh water and saline marshes and progressively higher (absolute maximum 867 percent) toward the brackish marshes.

(3) In the marshes proper the organic content is relatively low in fresh water and saline marshes but very high (59 percent) in the brackish marsh.

(4) In general the amount of organic material in the upper 12 inches of soil is approximately 50 percent greater than it is in the next lower foot of soil.

d. Salt tolerance.

(1) On the basis of relations to salinity the plants of swamp and marsh communities may be divided into halophobes (fresh water only), facultative halophytes, and true halophiles (salt water only). Certain plants have a narrow range of salt tolerance but most of the species range widely.

(2) In probable order of salt tolerance the major marsh dominants are: *Mariscus jamaicensis, Scirpus californicus, Typha latifolia, Typha angustifolia, Spartina patens, Juncus roemerianus, Spartina alterniflora,* and *Distichlis spicata.*

e. Of the bitoic factors man is of greatest importance due to his activity in canalization, reclamation projects and periodic firing of the marshes.

6. *Phenology.*

a. Six stages are recognized as follows: *pre-vernal* (February and early March); *vernal* (most of March, all of April); *estival* (May, June, July); *autumnal* (August, September); *post autumnal* (October, November); *hiemal* (December, January).

b. The total period of anthesis in true marsh communities is usually about 10 months, but in forest communities it may include every month of the year.

c. Certain species bloom continuously for 8 months, others, less than 3 weeks; still others exhibit two blooming periods, usually in early spring and late autumn.

d. The number of species in flower is small during the pre-vernal period; it increases rapidly during the vernal aspect, and reaches a maximum during the estival aspect. It attains a secondary peak in the autumnal aspect, but declines gradually during the post-autumnal period to scattered specimens or none in the hiemal aspect.

e. The maxima of anthesis in the marshes proper are estival; those in the zonal communities (shrub, cane, and salt grass belts) are vernal and autumnal.

f. The initiation of blooming, for the greatest number of species, occurs in the vernal aspect, although there is a secondary peak in the autumnal period. In general the onset of anthesis is earlier in the zonal communities than in the true marsh associes.

g. The greater the salinity of a marsh, the later is the onset of anthesis for the majority of its species and the later is the maximum anthesis of the community. However, each individual species tends to bloom *earlier* in the more saline parts of its range.

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CHARACTERISTICS OF MAJOR GRASSLAND TYPES IN WESTERN NORTH DAKOTA[1]

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[1] North Dakota Agricultural Experiment Station. Journal Series No. 25.

[2] The authors are indebted to Charles E. Kellogg and Kenneth Ableiter of the U. S. Soil Survey, E. H. Tyner, D. S. Dedrick for advice and suggestions; for correlation of soil types to Max Edwards and E. H. Tyner; and to several assistants employed on W.P.A. and N.Y.A. funds for aid in conducting laboratory determinations. The senior author is especially grateful to the National Research Council for grants-in-aid, without which it would have been impossible to conduct this research.

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CHARACTERISTICS OF MAJOR GRASSLAND TYPES IN WESTERN NORTH DAKOTA

INTRODUCTION

Knowledge of variation in botanical composition of grassland, as well as the causes and consequences of the variation, is basic to scientific land management. Striking differences in vegetation are characteristic of the badlands along the Little Missouri River in western North Dakota (Fig. 1). Some of the conspicuous vegetation types are mixed prairie on uplands, little bluestem on hillsides, saltgrass and sagebrush on stream terraces, sandgrass on hills, and woodland along stream courses. Following preliminary observations in 1932 and 1933, detailed study was started in 1934 and continued at greater length in the more favorable season of 1935. The objects were to determine the composition, frequency, and abundance of species in several examples of different types, to study soil and other conditions in each, and to classify the areas studied into types on the basis of data collected.

This study was conducted chiefly in the vicinity of Sentinel Butte and Medora in western North Dakota, in an unglaciated section of the northern

FIG. 1. View of Little Missouri Region about 16 miles southeast of Sentinel Butte. Trees are mostly ash, with Symphoricarpos, Rosa, Ribes, and Prunus between; dark areas on slopes little bluestem type; light areas on slopes western wheatgrass-grama-sedge type, sagebrush in valley of Garner Creek in middle distance at left, and grama-needlegrass-sedge type on plateau tops. August 31, 1935.

plains. The elevation was 2,000 to 2,600 feet for most of the test areas. The soils had developed from yellow and ash-gray shales, sandstones, and clays of the Fort Union formation of the Tertiary age or from alluvium derived from them. The Fort Union also contains numerous beds of lignite and baked shale and sandstone, called "scoria," produced by burning lignite beds. (Gauger et al, 1930.)

The soils of this region are in the Pedocal group according to Marbut's (1928) classification, and the general soil region is that of the dark-brown soils, which, south of the glacial boundary, are classified as the Rosebud series. The most important series in the Dark Brown Zonal Group are the Morton, in which the parent material is residual and the Farland, developed from general alluvium. The Patent, from local alluvium, and the Bainville from residual material are the light-colored immature soils associated with the more broken relief (Ableiter).

Due to erosion by wind and water and burning lignite veins there is great heterogeneity in topography, as plateau tops, slopes, terraces, valleys, buttes, low hills, and knobs of numerous shapes.

The mean precipitation is about 15 inches, (range 6-23) about 40 percent falling in May and June and only 12 percent during November to February, inclusive. The annual mean temperature is 41°F. July is the hottest month with a mean of 68.5°F. Prevailing winds are northwest (Roberts, 1935). The precipitation at the Olstad Ranch during the spring and summer of 1935 was: March, 1.02 ins.; April, 1.70; May, 2,25; June, 2.33; July, 3.33; and August, 1.12.

METHODS

Considerable time and care were devoted to selecting test areas which were sufficiently large, uniform in topography and vegetation, and free from harmful effects of grazing, mowing, and trampling. Usually the areas were located in winter-grazed pastures, in ungrazed portions of land adjoining cropped fields or in lightly grazed pastures. The test areas varied in size from about 2 to 20 acres. Homogeneity was considered of greater importance than size.

The frequency, abundance, and herbage cover of species were determined by the frequency-abundance and point methods (Hanson, 1935; Levy, 1933). In the former 30 m^2 sample areas and in the latter a total of 300 points were used in each test area. A total of about 900 square meter sample areas were used in this study. The data showing results of these botanical analyses are given in Tables 1 and 2.

A trench was dug in a carefully selected, typical place in each area after the vegetation had been studied. The soil profile and root system were examined and described from the sides of the trench. Samples of soil were taken from each horizon for laboratory analyses. Effervescence was tested in the

TABLE 1. Classification of 36 test areas into types and the frequency X abundance of chief species, 30m² quadrats for each test area. T—is less than 0.5, D—dominant, A—abundant, F—frequent, S—scarce. Test area 14* is similar to 15 and 17 but is transitional to Type 1 because of slightly higher elevation.

Species	TYPE 1 Bouteloua, Stipa, Carex							TYPE 2 Agropyron, Bouteloua, Carex				TYPE 3 Andropogon scoparius			TYPE 4 Calamovilfa				TYPE 5 Artemisia cana			TYPE 6 Distichlis, Agropyron			TYPE 7 Distichlis, Puccinellia		TYPE 8 Buchloe	TYPE 9 Andropogon furcatus					TYPE 10 Miscellaneous			
	1	2	3	4	6	7	36	10	11	12	13	25	26	31	21	22	23	24	18	19	20	15	17	14*	16	35	33	27	28	29	32	30	5	8	9	34
Bouteloua gracilis	95	100	95	100	93	91	D	100	75	100	100	3	2	S	47	13	28	28	75	..	48	15	65	95	....	A	S	1	...	...	...	13	74	100	100	D
Agropyron smithii	5	9	66	8	2	T	F	100	63	55	91	3	1	S	T	T	....	1	67	98	100	97	100	67	T	...	A	1	1	....	S	2	74	88	74	S
Stipa comata	98	79	46	70	95	29	L	1	6	16	..	....	T	..	44	30	42	26	2	2	1	1	1	64	....	....	.....	..	T	T	..	3	56	57	71	S
Koeleria cristata	47	8	1	1	....	33	..	....	1	2	..	10	4	S	10	15	17	25	....	....	....	....	....	T	....	....	.....	1	5	12	S	12	4	17	9	...
Carex filifolia	49	100	65	28	71	T	F	97	66	85	78	23	3	F	84	43	55	16	....	....	....	....	....	7	....	....	.....	T	1	T	..	4	11	8	27	...
Carex stenophylla	59	9	25	} 36	} 13	} 67	} A	...	2	...	...	} 14	} 8	...	1	...	} 54	...	....	....	....	....	....	....	....	....	S	} 12	...	53	..	T	28	19	14	...
Carex pennsylvanica	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	86	....	93	....	....	....	....	....	....	....	....	.....	....	47	....	....	51	....	....	....	....
Andropogon scoparius	....	....	....	....	....	8	..	....	....	....	....	100	100	D	18	2	....	16	....	....	....	....	....	....	....	....	.....	95	33	70	F	6	....	....	....	....
Calamovilfa longifolia	4	....	....	2	....	13	..	....	....	....	....	1	4	S	40	56	54	84	....	....	....	....	....	....	....	....	.....	....	T	....	....	22	....	....	....	....
Calamagrostis montanensis	12	....	1	11	8	2	F	....	....	....	....	T	....	....	1	....	....	T	....	....	T	....	....	5	....	....	.....	....	....	T	..	1	....	....	....	....
Andropogon furcatus	....	....	....	....	....	T	..	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	95	100	100	D	46	....	....	....	....
Distichlis stricta	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	46	88	45	100	D	.....	....	....	....	....	....	....	....	....	....
Stipa spartea	....	....	....	....	....	3	..	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	....	1	....	....	21	....	....	....	....
Stipa viridula	....	....	....	....	....	....	....	....	....	....	....	....	T	..	....	....	....	....	48	4	50	..	8	..	....	....	S	T	....	....	S	2	....	2	2	S
Bouteloua curtipendula	....	....	....	....	....	....	....	....	....	....	....	9	8	..	....	....	....	....	....	....	....	....	....	....	....	....	.....	22	1	5	F	1	....	....	....	....
Puccinellia nuttalliana	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	70	D	.....	....	....	....	....	....	....	....	....	....
Hordeum jubatum	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	22	....	.....	....	....	....	....	....	....	....	....	....
Sporobolus heterolepis	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	....	....	....	....	51	....	....	....	....
Plantago purshii	....	....	13	3	T	T	..	25	45	2	....	T	....	....	....	....	T	....	2	....	....	1	....	1	....	....	.....	....	....	....	....	....	23	T	....	....
Draba nemorosa	....	....	T	2	....	....	....	13	6	....	....	T	....	....	1	....	....	....	2	....	....	2	....	T	....	....	.....	T	....	....	....	....	10	....	....	....
Artemisia cana	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	29	90	24	....	1	....	....	....	.....	....	....	....	....	....	....	....	....	....
Juncus balticus	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	....	....	....	....	8	....	....	....	....
Buchloe dactyloides	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	D	....	....	....	....	....	....	....	....	....
Poa buckleyana	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	S	....	....	....	....	....	....	....	....	A
Miscellaneous grasses	3	2	4	....	T	10	..	1	....	1	T	4	1	....	6	1	1	21	1	2	5	7	....	T	1	....	.....	1	5	2	S	14	3	T	1	...
Miscellaneous forbs	65	29	23	40	22	39	..	16	16	9	4	28	13	....	15	7	16	12	5	5	19	22	2	36	15	....	.....	28	41	24	..	40	23	4	11	...
Total no. species 30m² quadrats	46	42	33	50	44	53	..	20	29	24	12	52	46	....	42	40	42	35	50	31	23	36	28	33	24	....	.....	55	63	41	..	86	42	18	24	...
Average no. species 30m² quadrats	17	10.9	12.3	19.2	11.5	16.9	..	10.3	11	6.8	3.7	12.8	10.8	..	12.6	9.9	10.7	10.2	12.9	6.1	5.2	7.9	5	9.2	6.6	..	.....	13	17.1	12.2	..	20.3	13.8	6.1	7	..

*Intermediate to Type 1 (See p. 89)

TABLE 2. Percentage of herbage cover of chief species and of bare ground in a total of 300 points for each test area, according to the point method. Same test areas as in Table 1.

Species	Type 1 Bouteloua, Stipa, Carex						Type 2 Agropyron, Bouteloua, Carex				Type 3 Andropogon scoparius	Type 4 Calamovilfa				Type 6 Distichlis, Agropyron			Type 7 Distichlis, Puccinellia	Type 9 Andropogon furcatus		Type 10 Miscellaneous		
	1	2	3	4	6	7	10	11	12	13	25	21	22	23	24	15	17	14	16	27	29	5	8	9
Bouteloua gracilis	26	36	37	43	17	19	27	23	32	47		8	4	5	6	5	22	31				29	53	50
Agropyron smithii	3	4	12	1			30	35	31	28			T		T	59	45	23				28	20	25
Stipa comata	25	20	15	19	22	7		3	2			16	7	17	5		T	20			T	12	7	11
Koeleria cristata	6					9					2		2	3	4						3		1	T
Carex filifolia	10	22	16	1	12	T	22	12	17	17	8	11	6	7	2			1				5	6	
Carex stenophylla	13	4	6	14	10	27		6			4			19						17	12	7	7	3
Carex pennsylvanica													27		27									
Andropogon scoparius						3					49	3								13	17			
Calamovilfa longifolia						14						33	42	34	45									
Calamagrostis montanensis	3																							
Andropogon furcatus																				53	58			
Distichlis stricta																13	22	10	52					
Stipa spartea						3																		
Stipa viridula																	3						T	
Bouteloua curtipendula											6										3			
Puccinellia nuttalliana																			27					
Hordeum jubatum																			6					
Miscellaneous grasses		1	1	2	4	2		1	1		1	10	1	1	3	1	1			5	T	2	T	1
Miscellaneous forbs	10	3	3	15	9	8	8	8	1	1	8	6	3	5	3	11	1	2	5	10	4	7	2	1
Bare ground	4	10	10	5	26	8	13	12	16	7	22	13	8	9	5	11	6	13	10	2	3	10	10	3
Total hits of vegetation	410	450	425	490	340	564	392	436	392	334	296	413	436	465	489	274	482	432	455	555	429	495	389	472

field with dilute HCl solution. Complete profile descriptions were made for each area but only a few typical ones are included in this paper.

Mechanical analyses of the soil samples were made by the Bouyoucos hydrometer method (1935). In many of the analyses sodium silicate was used as a deflocculating agent (Thoreen, 1933). Classification and terminology of soil texture are those used by the Bureau of Chemistry and Soils as described by Davis and Bennett (1927). Moisture-holding capacity was determined by the use of Hilgard soil pans (Duggar and Helgeson, 1933).

Total soluble salts were determined by the use of an electrolytic bridge, essentially similar to that described by Davis (1927). Soil reaction was determined electrometrically by means of the quinhydrone electrode for pH values up to 8.0 (Snyder, 1935), while above this cresol red and thymol blue were used as indicators in the colorometric method. The soil extract was obtained by the use of a sodium chloride leaching solution described by Morgan (1932).

Loss-on-ignition procedure followed Wright (1934), carbonate determinations according to Mehlich et al (1933), and tests for water-soluble nitrate nitrogen, phosphorus and chloride and exchangeable potassium, calcium, and sodium, according to procedures described by Morgan (1935).

The results of the soil determinations are presented in Table 3.

DESCRIPTIONS OF TEST AREAS

Each of the test areas is briefly described because variations occur between any pair that may be selected. The most accurate classification of vegetation is dependent upon comparing differences and similarities of selected areas which are studied in detail. The areas which show sufficient similarity to one another in essential characteristics are then naturally classified in one group. The differences between individual test areas are important in showing the variation within a group. The individual areas are also of importance in indicating that land use management must be based upon characteristics of individual areas, and not only upon generalized types. It is one of the duties of ecological research to describe these variations and to show how scientific classifications of vegetation must be based upon qualitative and quantitative data.

TEST AREA NUMBER 1 (JUNE 16, 1935)

This test area was located on a gentle, upland, south-facing slope, 10 miles northwest of Sentinel Butte in T. 141, R. 104. The dominants were Bouteloua, Stipa, and Carex. As indicated by the topography and by the sandstone and scoria particles in the parent material, the soil has developed from material eroded from former buttes or hills. This area is typical of much land cropped to wheat.

DESCRIPTION OF A TYPICAL UPLAND PROFILE IN MORTON FINE SANDY LOAM

Inches	
0- 1	Dark brown, fine sandy loam forming fine, crumb-like mulch. Very few roots.
1- 7	Dark brown, fine sandy loam. Coarse, friable crumb structure. Grass roots very numerous.
7-17	Brown, fine sandy loam distinctly lighter in color than the above horizon. Coarse, blocky structure breaking into angular fragments up to 1 x 2 x 0.5 inches.
17-20.5	Transitional horizon, light brown, fine sandy loam, effervescing[1] moderately.
20.5-32	Light brown, fine sandy loam becoming lighter colored with depth. Digs out in coarse angular fragments, readily friable. Effervescence moderate. Roots numerous but decreasing.
Below 32	Parent material. Light grayish brown, fine sandy loam with particles of sandstone and scoria intermixed, in the upper part somewhat cemented with carbonates which occur in streaks and blotches throughout. Effervescence strong. Roots of *Carex filifolia* more numerous in the parent material than those of other species. Roots decreased rapidly below 32 inches to working depth at 40 inches.

On June 16 the moisture of recent rains had penetrated to 32 inches. It was dry below.

The scarcity of *Agropyron smithii,* the presence of Calamovilfa, the abundance of Bouteloua, Stipa, Koeleria, *Carex* spp., and forbs; the high number of species (46) found in the test area and per quadrat (average of 17) appear to be associated with the uniform sandy loam soil which permitted excellent moisture penetration and root development to a working depth of 40 inches, freedom from salinity, absence of shallow carbonate layer, and the friable structure and dark brown color of the well-developed solum which extended to a depth of 20.5 inches. Vegetation development and soil development were apparently nearing maturity. Factors responsible for this development were freedom from continued overgrazing, cultivating, excessive mowing, and serious erosion.

TEST AREA NUMBER 2 (JUNE 18, 1935)

Test area number 2, typical of old uplands which are under cultivation, was located on a nearly level plateau top 7 miles east of Medora (Sec. 31, T. 140, R. 100). The dominants were Bouteloua, Carex, and Stipa. The soil, Morton fine sandy loam type, had developed from parent material residual from sandstone.

The abundance of *Bouteloua gracilis, Stipa comata, Carex filifolia,* and the forbs; the scarcity of *Agropyron smithii;* and the fairly large number of species in the area appear to be associated with the well developed solum which was brown in color, 23 inches deep and with structure favorable to

[1] Effervescence in soils indicates the presence of free $CaCO_3$.

root growth; sandy loam texture in both solum and parent material; level topography which reduced runoff and erosion to a minimum; and freedom from excessive salt concentration. Both soil and vegetation were mature or nearly so. The deeper solum, the absence of *Calamagrostis montanensis* and Calamovilfa, and the more pronounced carbonate layer indicate that this test area was more mature than number 1.

TEST AREA NUMBER 3 (JULY 27, 1935, FIG. 2)

This area was located on a fairly level plateau top, on the Olstad Ranch, about 15 miles southeast of Sentinel Butte (Sec. 5, T. 138, R. 103). The dominants were Bouteloua, Agropyron, Carex, and Stipa. The soil type was Morton clay loam.

The decrease in abundance and cover of *Stipa comata* and *Carex filifolia* in this area as compared with test areas 1 and 2, the increase in *Agropyron smithii*, the abundance of *Bouteloua gracilis*, and the shallower working depth of roots (30 inches) were associated with heavier soil (29.7 percent clay to working depth compared to 9.9 and 14.1 in areas 1 and 2), higher moisture-holding capacity, higher content of carbonates especially in the 14 to 24-inch layer, and a pronounced carbonate layer between 31 and 33 inches. Although

FIG. 2. Test area number 3, grama-needlegrass-sedge type on plateau about 15 miles southeast of Sentinel Butte. White fruiting stalks of *Stipa comata* are conspicuous against the darker background of *Bouteloua gracilis*, *Agropyron smithii*, and *Carex* spp. July 26, 1935.

runoff and erosion were negligible on this nearly level plateau, the solum was only 14 inches deep.

TEST AREA NUMBER 4 (AUGUST 3, 1935)

Test area 4 was located on a school section (state owned) in the gently rolling, upland prairie 4 miles west of Dickinson. The dominants were Bouteloua, Stipa, and Carex. The soil type was Morton sandy loam. Land of this kind is mostly under cultivation in this region.

The great variety of species (50 in 30 m^2 quadrats) and the dominance of *Boutcloua gracilis, Stipa comata,* and Carex were associated with soil texture mostly sandy loam, well developed solum to depth of 33 inches which was acid in reaction to a depth of 22.5 inches, deep carbonate zone at 45 to 50 inches, and freedom from excessive runoff and erosion. The shallow working depth of roots (28 inches) may have been caused by death of deeper roots due to droughts in recent years. The texture and color of the solum and the character of the vegetation are characteristic of approximate maturity of soil and vegetation. The high proportion of sand in this soil indicates that continuous cultivation may result in serious wind erosion.

TEST AREA NUMBER 5 (JULY 1, 1935)

This area was located on a fairly level, upper terrace about 10 feet above a creek, on the Olstad Ranch 16 miles southeast of Sentinel Butte (Sec. 4, T. 138, R. 103). The dominants were Bouteloua, Agropyron, Stipa, and Carex. The parent material was alluvium.

DESCRIPTION OF A TYPICAL PROFILE IN AN UPPER TERRACE IN GORHAM SANDY LOAM

Inches	
0- 2	Dark brown, sandy loam; loose and friable, mulch-like. Roots few. rhizomes numerous.
2- 7	Dark brown, sandy loam with coarse, angular fragmentary structure. Pieces are 1/2 to 3/4 in. in diameter, readily friable. Accumulation of scoria particles and yellowish chalky material occurs at the bottom of this horizon. Roots very numerous.
7-21	Light brown, clay loam streaked with organic matter above. Prismatic structure, moderately effervescent. Roots numerous.
21-30	Light yellowish brown, sandy clay loam. Blocky structure, soil falling out in irregular angular pieces, readily friable. Effervescence moderate, roots very numerous.
30-33	Light brown, clay. Nearly structureless, very hard, streaked and mottled with carbonates. Moderately strong effervescence, most roots end here.
33-38	Dark brown, silty clay. Soil falling out in vertically elongated pieces up to 3 inches. Effervescence moderate, dead roots rather numerous. Carbonate flecks numerous. Probably represents a buried soil horizon.
38-59	Light olive gray, alternate layers of clay and fine sand, effervescing moderately with HC1. Carbonate region conspicuous at 55 inches. Roots become scarce at 59 inches. Working depth of roots is 28 inches.

The heterogeneity of the soil is pronounced, varying from sandy loam to clay, from a carbonate content of 7.7 percent in the surface 2 inches to 20.8 percent at 38 to 59 inches, total soluble salts from 428 p.p.m to 6,300. In addition the profile shows a former surface layer at 33 to 38 inches. The present solum is only about 7 inches deep. The vegetation on this heterogeneous and youthful soil was characterized by the abundance of *Agropyron smithii* and *Bouteloua gracilis,* the presence in much smaller numbers of *Stipa comata,* Carex and *Koeleria cristata;* fairly large numbers of *Plantago purshii* and *Draba nemorosa;* and a fairly high total number of species. Frequently land similar to this area is under cultivation.

FIG. 3. Test area number 6, grama-needlegrass-sedge type on upland slope 26 miles southwest of Belfield. Dark stalks of *Artemisia dracunculoides* and white stalks of *Stipa comata* are conspicuous against the darker, shorter growth of *Bouteloua gracilis* and *Carex* spp. July 30, 1935.

TEST AREA NUMBER 6 (JULY 30, 1935, FIG. 3)

This area was located on a north-facing slope (5 to 10°), on the road to Ranger, 26 miles southwest of Belfield. The dominants were Bouteloua, Stipa, and Carex. The soil, Morton sandy loam (rolling phase) type, had developed apparently from sand of residual origin.

The abundance of *Bouteloua gracilis, Stipa comata,* Carex, and forbs, the fairly high total number of species on the area, the scarcity of *Agropyron smithii,* and the high percentage of bare ground (26 percent) were associated with a well-developed solum to a depth of 22 inches which is very sandy (70-82 percent); parent material composed chiefly of sand (83-87 percent); north-facing slope; freedom from excessive runoff and erosion; relatively low mois-

ture holding capacity (39-62 percent), low loss-on-ignition below 13 inches (1.7-2.8 percent), moderately high carbonate content (7.5-11 percent), and low concentration of soluble salts. The absence of Calamovilfa on this sandy soil was noteworthy.

TEST AREA NUMBER 7 (AUGUST 6, 1935)

This area was located on a gentle south-facing slope, (less than 5°) 8.5 miles north of Grassy Butte (Sec. 31, T. 147, R. 199). The dominants were Bouteloua, Carex, Koeleria, Calamovilfa, and Stipa. The soil, Morton sandy loam type, appeared to have been developed from parent material residual from sandstone. Much land similar to this is under cultivation.

PROFILE DESCRIPTION

Morton sandy loam

Inches

0-1.5 Dark brown to black, sandy loam. Pulverulent, readily friable. Roots numerous.

1.5- 3 Dark brown, sandy loam. Breaks into small clod-like fragments 1/4 to 1/2 inch in diameter, readily friable. Roots very numerous.

3-7.5 Dark brown, sandy loam. Prismatic structure, prisms 1 to 2 inches in diameter, very hard, breaking into irregular nut-sized pieces which are friable with difficulty to crumb. Roots numerous, follow cleavage planes mostly.

7.5-18 Brown, sandy loam. Poorly defined prismatic structure, becoming indistinct with depth. Prisms break into angular chunks 1/2 to 1 inch in diameter, more friable than the above horizon. Roots numerous, decreasing rapidly below 14 inches.

18-38 Brown sandy loam. Blocky structure, the soil falling out in angular pieces up to 1 inch in diameter and 2 inches long. Roots moderately numerous.

38-44 Tan colored, sandy loam. Irregular pieces falling readily into single grains, roots few.

44-60 Light tan sand, loose, roots scarce. No effervescence as deep as 60 inches.

This area was well developed prairie composed of 16 species of grasses and sedges and 37 species of forbs with an average of 16.9 species per meter square quadrat. The chief species were *Bouteloua gracilis, Carex stenophylla, C. pennsylvanica, Calamovilfa longifolia, Koeleria cristata, Stipa comata, Artemisia gnaphalodes,* and *Psoralea argophylla.* The presence of *Stipa spartea, Andropogon furcatus,* and *A. scoparius,* although in small numbers, indicated favorable conditions for prairie species. The sandy loam soil and gentle slope permitted ready penetration of precipitation. As indicated by the dark brown color and prismatic structure the solum was well developed, extending to a depth of 38 inches. Other distinctive aspects of the soil were high moisture holding capacity (62.8-64.8 percent) in the surface 7.5 inches for

a soil with such a high proportion of sand (58 percent), soil reaction mildly acid to depth of 27 inches, and the lack of excessive carbonates as tested by HCl to depth of 60 inches. The abundance of Calamovilfa and the scarcity of *Carex filifolia* in this area, and *vice versa* in area 6, may be due to lack of deep soil moisture in area 6, caused in part by the dominance of shallow-rooted grasses in number 6, while in this area deep moisture is probably present throughout most of the growing season. In area 7 the shallow-rooted plants were much less abundant than in area 6.

TEST AREA 8 (JUNE 20, 1934)

A long slope falling gently away from eroded buttes, 5 miles south of Sentinel Butte, was the site of this area (Sec. 9, T. 139, R. 104). The dominants were Bouteloua, Agropyron, and Stipa. The soil type was Patent clay.

The abundance of *Bouteloua gracilis* and *Agropyron smithii*, the scarcity of other grasses, and the small total number of species were associated with the high proportion of clay in the soil (averaging 46.5 percent to the working depth), gradual slope, shallow solum and carbonates and a pronounced carbonate layer at 34 to 44 inches. The severe drought of 1934 very likely decreased the number of species of forbs that might usually occur on this area.

TEST AREA 9

This area was located about 3 miles from area number 8 (Sec. 8, T. 139, R. 104). In topography, soil, and vegetation it was very similar to number 8. The dominants were Bouteloua, Agropyron, Stipa, and Carex. Only analyses of the vegetation were made in this area.

TEST AREA 10 (JUNE 17, 1935)

This area was located on a long, sweeping slope 11 miles northeast of Sentinel Butte (Sec. 35, T. 141, R. 103). The dominants were Agropyron, Bouteloua, and Carex. The soil originated, it appears, from outwash material eroded from a butte, of which only a remnant now remains. Much land similar to this is under cultivation and cropped chiefly to wheat.

DESCRIPTION OF A TYPICAL PROFILE IN A LONG GRADUAL SLOPE IN PATENT CLAY LOAM

Inches	
0 - 1	Dark brown, clay loam rich in organic matter. Fine crumby mulch, roots few to none.
1 - 4.5	Dark grayish-brown, clay loam. Slightly platy, effervescence moderately strong. Roots very numerous.
4.5-10.5	Light brown, clay. Soil breaks out in small nut-like fragments readily friable to small crumbs. Strong effervescence. Roots numerous.

10.5-27 Light grayish-brown clay. Blocky structure, soil falls out in hard angular fragments. Highly effervescent, roots fairly numerous to 22 inches, scarce below.

27 -50 Parent material. Light grayish-brown clay, compact and heavy, with small rock particles. Carbonates occur in streaks and blotches. Violently effervescent, roots infrequent, soil forms hard chunks when dry. Working depth of roots is 25 inches.

The abundance of *Agropyron smithii, Bouteloua gracilis,* and *Carex filifolia;* the scarcity or absence of other species of grasses; the low number of species on the area and per quadrat are associated with clay soil, shallow solum, carbonates within one inch of the surface and becoming pronounced at only 4.5 inches, high loss-on-ignition, alkaline reaction throughout and vegetation cover usually preventing excessive erosion. Soil and vegetation evidently have not reached maturity. Under cultivation this area would be subject to increased runoff and erosion.

TEST AREA 11 (JULY 5, 1935)

This test area on the Olstad Ranch, about 16 miles southeast of Sentinel Butte, was located on a long slope which stretched from the hills to a low terrace along an intermittent stream (Sec. 33, T. 139, R. 103). The dominants were Agropyron, Bouteloua, and Carex. The soil, Patent clay loam type, originated probably from material washed down from hills, now largely eroded away.

The abundance of *Bouteloua gracilis, Agropyron smithii,* and *Carex filifolia,* the scarcity or absence of other grasses, the fairly low total number (29) of species, were associated with clay loam to clay soil, shallow solum (14.5 inches), carbonates within 3.5 inches of the surface and a compact layer at 26 to 47 inches, alkaline reaction throughout, high calcium content, long gradual slope, and usually only moderate erosion. Soil and vegetation appear to be somewhat more developed than in area 10.

TEST AREA 12 (AUGUST 13, 1935, FIG. 4)

This area was located on the Olstad Ranch about 15 miles southeast of Sentinel Butte on a long gradual slope extending from a small upland plateau to a dry draw (Sec. 5, T. 138, R. 103). The dominants were Bouteloua, Agropyron, and Carex. The soil type was Patent clay loam.

The abundance of *Bouteloua gracilis, Agropyron smithii,* and *Carex filifolia,* the scarcity of other species of grasses, the fairly low total number (24) of species on the area and average number (6.8) per quadrat were associated with clay loam to clay except the surface 2 inches which have sandy loam texture, shallow solum (20 inches) alkaline reaction except surface 2 inches; carbonate content high beginning as shallow as 6 inches and extending as deep as dug (40 inches), long gradual slope and moderate ero-

FIG. 4. Test area number 12, western wheatgrass-grama-sedge type, is on the long slope in the foreground, test areas 26, little bluestem type and 27, big bluestem type, on the hillside in center. Sentinel Butte in the distance. August 12, 1935.

sion. The sandy loam texture of the surface 2 inches may be a factor in the small increases in *Stipa comata* and *Carex filifolia* and the small decrease in *Agropyron smithii* in this test area as compared with areas 10 and 11 which did not have sandy texture in the surface layers. The vegetation and soil do not appear to have reached equilibrium.

TEST AREA 13 (JUNE 19, 1934)

This area was located on a long gradual slope 4 miles south of Medora (Sec. 11, T. 139, R. 102). The dominants were Bouteloua, Agropyron, and Carex. The soil, Patent clay loam type, appeared to have originated from local alluvium eroded away from buttes above, remnants of which are now present.

The dominance of *Bouteloua gracilis, Agropyron smithii,* and *Carex filifolia,* the low total number (12) of the species on the area, the low average number (3.7) of species per quadrat, and the absence or extreme scarcity of other species of grasses were associated with clay to clay loam texture, shallow solum (21 inches), alkaline reaction throughout, and carbonates beginning at the surface and becoming pronounced at 15 inches. Vegetation and soil appeared to be less developed in this area than in areas 10, 11, and

12, due probably to more recent origin and the slightly steeper slope which would favor greater runoff and erosion.

TEST AREA 14 (JULY 25, 1935, FIG. 5)

This area was located on the Olstad Ranch about 16 miles southeast of Sentinel Butte on a low terrace 8 to 12 feet above a stream in which stood

FIG. 5. Test area 14 on the terrace, with dominants, *Bouteloua gracilis*, *Agropyron smithii*, *Stipa comata*, and *Distichlis stricta* and scattered *Artemisia cana*. In the foreground shrubs are chiefly Symphoricarpos, Rosa, and Ribes; in draws Prunus, Amelanchier, Fraxinus. Fisher Run, 16 miles southeast of Sentinel Butte. July 24, 1935.

occasional pools of water (Sec. 33, T. 139, R. 103). The dominants were Bouteloua, Agropyron, Stipa, and Distichlis. The soil originated from materials washed down from surrounding higher land.

DESCRIPTION OF A TYPICAL PROFILE IN A LOW TERRACE IN HUFF SANDY LOAM

Inches	
0 - 1	Dark brown, sandy loam. Friable, brittle crust. Soil reacts mildly on the surface with HCl. Roots and rhizomes few.
1 - 3	Dark brown, sandy loam. Platiness slightly developed, soil digs out in irregular chunks readily friable to fine crumb, small pieces of scoria intermixed. Effervescence moderate, roots and rhizomes numerous.
3 - 7	Brown sandy loam, coarse angular structure, pieces readily friable. Moderate effervescence, roots numerous, rhizomes few.
7 - 8.5	Fine gravel, sand, and small pieces of scoria. Moderate effervescence, roots numerous, rhizomes scarce.

8.5-15.5 Brown, sandy loam. Soil digs out in angular nut-sized fragments, readily friable, occasional black flecks of lignite occur in the upper part of the horizon. Moderate effervescence, numerous roots, rhizomes scarce.

15.5-54 Parent material. Brown, sandy loam. White flecks in the soil mass and white accumulations along roots and old root channels, small pieces of lignite and scoria are intermixed. Strong effervescence, roots numerous to 25 inches, becoming scarce at 40 inches. Below 40 inches coarse gravel, large pieces of scoria and very heavy, greasy, blue clay. Working depth of roots 26 inches.

The unusual mixture of *Bouteloua gracilis, Agropyron smithii, Stipa comata,* and *Distichlis stricta,* the moderate number of species on the area (33) and per quadrat (9.2) were associated with dominantly sandy loam to depth of about 40 inches, heavy clay intermixed with gravel below 40 inches, very shallow solum (7 inches), usually favorable soil moisture, high sodium and total soluble salt concentrations below 15.5 inches, high carbonate content beginning at surface, and terrace topography. As the stream erodes a deeper channel, Distichlis and Agropyron may decrease on this area.

TEST AREA 15 (JUNE 20, 1935)

This area was located on a low terrace about 5 to 6 feet above a small, usually dry creek, along U. S. Highway No. 10, 8 miles east of Sentinel Butte (Sec. 22, T. 140, R. 103). The dominants were Agropyron and Distichlis. Soil developed on alluvial material.

DESCRIPTION OF TYPICAL PROFILE IN LOW TERRACE IN GORHAM CLAY LOAM

Inches

0 - 3 Grayish-brown loam, recently deposited, stratified, breaks into small angular fragments readily friable. Effervescence moderate, roots and rhizomes very numerous.

3 - 4 Dark brown to black clay loam, apparently containing much organic matter. Slightly developed platiness, soil breaks into small, friable, angular fragments. Mild effervescence, roots and rhizomes very numerous.

4 - 6 Dark brown, silt loam, apparently rich in organic matter. Soil digs out in small, friable, angular fragments. Moderate effervescence, roots very numerous.

6 -11.5 Dark brown, silt loam. Coarse blocky structure, soil digs out in large friable, irregularly angled chunks. Small white carbonate pockets which effervesce violently, soil mass streaked with white showing only moderate effervescence. Roots numerous.

11.5-12 Dark brown to black, silt loam, apparently containing considerable organic matter. Former surface horizon having slight indications of a former platiness. Effervescence moderate, roots numerous, rhizomes few.

12 -20.5 Grayish-brown silt loam. Coarse blocky structure, soil digs out in large chunks which crumble readily to small angular fragments.

Effervescence moderate, roots numerous, rhizomes found down to 18 inches.

20.5-21 Another dark brown horizon, apparently rich in organic matter, roots numerous. This horizon is very similar to the 11.5 to 12 inch layer.

21 -60 Grayish-brown loam. Layer from 22 to 28 inches is hard, apparently contains much salt. Below 51 inches scoria and lignite particles intermixed, effervescence moderate. Working depth of roots 22 inches. Dead roots indicate that the working depth in previous years has been about 29 inches. Old root channels marked by incrustations of white salts.

The abundance of *Agropyron smithii* and *Distichlis stricta,* the scarcity of grasses as *Bouteloua gracilis* and *Stipa comata,* the moderate number of forbs (25) and of total species (36) on the area, the fairly low number (7.9) of species per quadrat were associated with soil texture of chiefly silt loam, high content of carbonates beginning at surface, fairly high concentration of soluble salts at surface and becoming greater below 6 inches, very high to medium high concentration of calcium, high moisture holding capacity especially in the 3 to 4-inch layer, alkaline reaction throughout, and usually ample moisture for plant growth fairly close to surface. The higher amounts of clay, salt, and moisture in the surface foot of soil in this area as compared to number 14, may account for the small amount of *Bouteloua gracilis* and *Stipa comata* and abundance of *Agropyron smithii.* Poor aeration below one foot may also be a factor.

TEST AREA 16 (JUNE 21, 1935)

This area was located on a flat bordering a shallow water course along U. S. Highway No. 10, 8 miles east of Sentinel Butte (Sec. 22, T. 140, R. 103). It was 4 or 5 feet lower than area 15. The dominants were Distichlis and Puccinellia. The soil, Gorham clay loam type, originated from water deposited material.

The abundance of *Distichlis stricta, Puccinellia nuttalliana,* and the presence of *Hordeum jubatum,* the scarcity of *Agropyron smithii,* the absence of other grasses as *Bouteloua gracilis* and *Stipa comata,* the fairly low number of total species on the area (24) and per quadrat (6.6) and the shallow working depth of the roots (now 18, formerly 26 inches) were associated with the loam to silty clay texture, high colloidal content, the unusually high concentration of soluble salts beginning at the surface and extending to 54 inches (1,587 to 11,100 p.p.m.), the high carbonate content throughout the profile (17.6 to 21.5 percent), the high calcium content, and, usually, the large amount of soil moisture close to the surface. Lack of aeration may also be an important factor.

TEST AREA 17 (JUNE 25, 1935, FIG. 6)

This area was located on a low terrace 8 to 10 feet above Garner Creek on the Olstad Ranch about 16 miles southeast of Sentinel Butte (Sec. 34, T. 139, R. 103). The dominants were Agropyron, Distichlis, and Bouteloua. The soil, Gorham sandy loam type, originated from material deposited by flood waters as in the summers of 1935 and 1929.

FIG. 6. Test area 17, saltgrass-western-wheatgrass type, on a terrace along Garner Creek, 16 miles southeast of Sentinel Butte. Trees are chiefly *Fraxinus pennsylvanica*, shrubs along creek are mostly *Symphoricarpos occidentalis*, *Rosa woodsii*, and *Ribes* spp. July 10, 1935.

The abundance of *Agropyron smithii*, *Distichlis stricta*, and *Bouteloua gracilis*, the presence of *Stipa viridula* and *Artemisia cana*, the scarcity of *Stipa comata*, the low total number (28) of species on the area and the low average number of species per quadrat, and the scarcity of forbs were associated with chiefly loam texture, high concentration of soluble salts, especially sodium, below 20 inches, large amounts of carbonates even in the surface soil, alkaline reaction throughout, and soil moisture usually plentiful near the surface and excessive below 2 or 3 feet. The smaller amount of *Stipa comata* on this area as compared with area 14, which is somewhat similar, may be due to excessive soil moisture and higher clay content.

TEST AREA 18 (JUNE 26, 1935)

Area 18 was located on a nearly level flat about 12 feet above Garner Creek on the Olstad Ranch, 16 miles southeast of Sentinel Butte (Sec. 5,

T. 138, R. 103). Although dominantly a sagebrush *(Artemisia cana)* type, it was well grassed. The dominants in addition to sagebrush were Bouteloua, Agropyron, and Stipa. The height of the sagebrush made it impracticable to use the point system. The material from which the soil developed was largely flood deposited.

DESCRIPTION OF TYPICAL PROFILE IN SAGEBRUSH FLAT IN CHERRY CLAY

Inches	
0- 2	Dark brown clay. Slightly developed platiness, readily friable, becoming light and puffy on being pulverized. Mild effervescence on surface, roots few, rhizomes frequent.
2- 7	Dark brown clay, definite platy structure, friable. Moderate effervescence, roots numerous, rhizomes frequent.
7-11	Brown clay, prismatic structure, breaks into small nut-like chunks 1/2 to 1 inch in diameter, friable. Effervescence moderate, increasing with depth, roots very numerous.
11-18	Light brown clay, coarse prismatic structure, falls out in large friable chunks up to 2 inches in diameter. Effervescence moderate, somewhat stronger than in above horizon, roots numerous.
18-27	Light brown clay, blocky structure, digs out in irregular chunks up to 4 inches long and 2 inches in diameter. A hard, compact layer. Effervescence moderate to violent, streaks of carbonate appear in the lower part of the horizon. Roots fairly numerous, particularly of sage, other roots follow sage roots.
27-61	Parent material. Light brown clay, stratified, very hard and dry, marked throughout with white streakings. Strong effervescence, grass roots few, sage roots continue to below 60 inches. Working depth of roots 31 inches.

The abundance of *Artemisia cana, Bouteloua gracilis, Agropyron smithii,* and *Stipa viridula,* the large number (50) of total species on the area, and the low frequency-abundance of forbs were associated with soil mainly clay in texture, soluble salts not excessive, carbonates fairly high below 11 inches, high loss-on-ignition of surface 11 inches, alkaline reaction throughout, solum 18 inches deep, nearly level topography, and subsoil moisture available throughout season, at least below 5 feet. The absence of Distichlis may be due to lack of excessive soluble salts and moisture in the surface 2 to 3 feet.

TEST AREA 19 (JUNE 19, 1935, FIG. 7)

A narrow valley, subject to frequent flooding following rains, 4 miles north of Medora and about a quarter of a mile from the Little Missouri River was selected for this area (Sec. 29, T. 141, R. 101). The vegetation was predominantly *Artemisia cana.* Because of the height and spread of the sagebrush it was impracticable to use the point method. The parent material had mostly been deposited from flood waters.

FIG. 7. Test area 19, sagebrush type, about 4 miles north of Medora. June 19, 1935.

DESCRIPTION OF A TYPICAL PROFILE OF SAGEBRUSH FLAT IN MEDORA SILT LOAM

Inches	
0 - 0.5	Light gray, silt loam, recently deposited, stratified, forming dry powdery surface crust which blows readily. Mild effervescence, no roots.
0.5-12.5	Grayish-brown, silt loam, stratified, occasional scoria pockets. Moderate effervescence, roots numerous.
12.5-48.5	Gray, uniform deposit of silty clay loam, laminated, occasional small pockets of lignite particles. Moderate effervescence, roots numerous.
48.5-53	Grayish, sandy loam containing numerous small particles of scoria. Moderately strong effervescence, roots numerous.
53 -64	Very fine sand and silt, laminated, occasional streaks of fine coal particles, moderate effervescence. Working depth of roots 52 inches. Roots fairly numerous again between 60 and 65 inches.

The abundance of *Artemisia cana* and *Agropyron smithii*, the presence of *Stipa viridula* and *Stipa comata*, the scarcity of forbs and other species of grasses, the moderate number (31) of total species on the area, and the low average number per quadrat were associated with recently deposited silt loam to 4 feet in depth, slightly alkaline reaction throughout, somewhat greater concentration of soluble salts than in the similar area number 18, fairly high carbonate content beginning at the surface, small amount of so-

dium below 4 feet, and moisture usually available below 4 or 5 feet. As in area 18 the lack of excessive salts and moisture within the surface 2 or 3 feet may account for the absence of Distichlis.

TEST AREA 20 (JUNE 22, 1934)

This area was located on a large flat along the Little Missouri River just north of the mouth of Garner Creek (Sec. 28, T. 139, R. 102). The dominance of sagebrush made it impossible to use the point system. Agropyron, Bouteloua, and *Stipa viridula* were dominants between the sagebrush. The soil type was Medora clay loam. Parent material has been recently deposited, chiefly by flood waters.

The abundance of *Artemisia cana, Agropyron smithii, Bouteloua gracilis,* and *Stipa viridula,* the moderate abundance of forbs, the small number (23) of total species, and the low average number (5.1) of species per quadrat were associated with recently deposited clay or silty clay to depth of 25.5 inches underlaid by fine sandy loam, alkaline reaction throughout, carbonates beginning at the surface and maximum concentration at 25.5 to 29.5 inches; and subsoil moisture available throughout season only below 3.5 feet or more.

TEST AREA 21 (JULY 15, 1935)

A sandy, upland ridge on the Olstad Ranch about 16 miles southeast of Sentinel Butte was selected (Sec. 4, T. 138, R. 103). The chief dominant was Calamovilfa.

DESCRIPTION OF TYPICAL PROFILE IN BAINVILLE FINE SAND

Inches	
0-6	Grayish-brown, fine sand, single grain structure, shows somewhat the influence of organic matter. Mild effervescence, rhizomes numerous in upper 3 inches, roots abundant below this.
6-64	Loose, undifferentiated, light grayish-brown, sandy loam with occasional pieces of scoria and friable sandstone intermixed. Moderate effervescence, roots numerous.
64-67	Light grayish-brown fine sand. Horizon of carbonate accumulation, strong effervescence, small granules of carbonate material effervesce violently. Roots numerous.
67-74	Light grayish-brown fine sand, loose, moderate effervescence. Working depth of roots at 70 inches, maximum depth below 10 feet.

The dominance and abundance of *Calamovilfa longifolia;* the abundance of *Carex filifolia, Stipa comata,* and *Bouteloua gracilis,* the presence of *Koeleria cristata, Andropogon scoparius, Andropogon hallii, Meriolix serrulata, Yucca glauca,* and other forbs, the scarcity of *Agropyron smithii,* the fairly large total number (42) of total species, and fairly large average number (12.6) per quadrat were associataed with soil texture of fine sand to

sandy loam, low soil colloid content, moderate moisture holding capacity, very low loss-on-ignition, alkaline reaction throughout, fairly high carbonate content throughout, low amount of total soluble salts, low calcium content, and usually available soil moisture throughout the season at some depth in the soil.

TEST AREA 22 (AUGUST 1, 1935, FIG. 8)

This area was selected on an 8° south-facing, upland slope, 25 miles southwest of Belfield along the Ranger road. Dominants were Calamovilfa and Carex. The parent material appeared to be residual in origin. The soil type was Bainville sandy loam (rolling phase).

FIG. 8. Test area 22, sandgrass type, on a south facing slope, 25 miles southwest of Belfield. August 1, 1935.

The abundance of *Calamovilfa longifolia* and *Carex pennsylvanica*, the fairly high frequency-abundance of *Stipa comata* and *Carex filifolia*, the presence of *Bouteloua gracilis*, *Koeleria cristata*, and *Andropogon scoparius*, the scarcity of *Agropyron smithii*, the fairly high total number (40) of species, and the moderate average number (9.9) of species per quadrat were associated with a highly uniform sandy loam texture, low colloidal content, moderate moisture holding capacity, small amount of soluble salts and carbonates, low loss-on-ignition, acid reaction throughout, medium amount of Ca throughout, very high concentration of K in the surface foot, fairly well developed solum to 19 inches, moderate slope well covered with plant débris so that runoff and erosion were negligible. Soil and vegetation on this area showed considerably more development than in area 21. It seems that Calamovilfa should be less abundant and *Stipa comata* more abundant on area 22 than on area 21 but the opposite was true. The higher carbonate

content and alkaline reaction throughout the profile in area 21 may be important factors. Grazing in the past, an unknown factor, may also be important in determining such differences. This emphasizes that long time records of all factors are essential in basic investigations.

TEST AREA 23 (JULY 31, 1935)

This area was located on an upland, south-facing slope (8 to 10°), 26 miles southwest of Belfield, along the Ranger road. The dominants were Calamovilfa, Carex, and Stipa. It was selected because it appeared to have less of the first and more of the last than area 22. The soil material appeared to be residual in origin. The soil type was Bainville (rolling phase).

The abundance of *Calamovilfa longifolia*, Carex, and *Stipa comata*, the presence of *Bouteloua gracilis* and *Koeleria cristata*, the absence of *Agropyron smithii*, the fairly high total number (42) of species on the area, the moderate average number (10.7) of species per quadrat were associated with sandy loam texture, fairly well developed solum to depth of 17.5 inches, moderately low amount of colloidal matter, fairly high moisture holding capacity, low loss-on-ignition, acid reaction to 42 inches, low amount of soluble salts and calcium, and gentle slope permitting ready penetration of water. Comparison of this area with number 6, which was located on the north facing slope of the same hill, shows that number 6 had more *Bouteloua gracilis* and *Stipa comata* and no *Calamovilfa longifolia*. The only important differences in soil conditions were that area 6 had a deeper solum (29.5 in.), higher sand content, and greater amount of carbonates especially below 22 inches. The direction of the slope may have been of major importance since the surface soil would dry more rapidly on the south-facing slope (area 23) than on the north-facing slope (area 6).

TEST AREA 24 (JUNE 25, 1934)

This area was located on a gentle upland slope (5 degrees or less), facing south to southeast, 9 miles southeast of Sentinel Butte (Sec. 7, T. 139, R. 103). Dominants were Calamovilfa and Carex. The soil type was Morton fine sandy loam.

The abundance of *Calamovilfa longifolia*, and *Carex* spp., the presence in moderate numbers of *Bouteloua gracilis*, *Stipa comata*, and *Koeleria cristata*, the presence in small numbers of *Andropogon scoparius*, *Aristida longiseta*, and *Panicum wilcoxianum*, the scarcity of *Agropyron smithii*, the moderate total number (35) of species on the area, and the moderate average number (10.2) of species per quadrat were associated with sandy loam texture, fairly low colloidal content of soil, acid reaction to 39 inches, solum moderately developed extending to 23 inches in depth, no effervescence to depth of 72 inches, and moderate slope permitting ready penetration of water.

TEST AREA 25 (JULY 20, 1935)

This area was located on the lower part of a 20 to 25° slope on the Olstad Ranch about 16 miles southeast of Sentinel Butte (Sec. 33, T. 139, R. 103). *Andropogon scoparius* was dominant.

DESCRIPTION OF TYPICAL PROFILE IN LITTLE BLUESTEM TYPE IN BAINVILLE FINE SANDY LOAM (STEEP PHASE)

Inches	
0-1.5	Dark brown sandy loam, fine crumb structure, moderate effervescence, roots few, rhizomes few.
1.5- 4	Dark Brown sandy loam. Soil forms small angular fragments which are friable to fine crumbs. Effervescence moderate but somewhat stronger than in horizon above, roots numerous.
4- 7	Brown silty clay loam, fragmentary structure. Angular fragments range from 1/4 to 3/4 of an inch in diameter, readily friable. Effervescence moderate, roots numerous.
7- 12	Dark gray silty clay, fragmentary structure. Angular fragments friable to fine light powder, strongly effervescent, roots numerous.
12- 53	Parent material. Gray silt loam, definitely stratified, streaked and mottled with iron stains. Strongly effervescent, roots numerous. Below 20 inches were alternate layers of fine sand and clay also stained and mottled. No definite zone of carbonate accumulation. Working depth of roots 26 inches. Roots very few at 53 inches.

The abundance of *Andropogon scoparius,* and the presence of numerous other species of grasses and forbs making a total of 52 on the area and an average of 12.8 per quadrat were associated with a fairly steep slope (20° to 25°), shallow solum (7 inches), texture of surface 4 inches sandy loam, underlaid by horizons of silty clay loam, silty clay and silt loam, high moisture holding capacity, and usually ample moisture for plant growth throughout the season at least below one foot, slightly alkaline reaction throughout, very high amounts of carbonates (21 to 30 percent) in all horizons except surface 1.5 inches, low amounts of soluble salts, and calcium content medium to high. Because of the fairly steep slope this area was subject to considerable runoff and erosion but the dense cover of vegetation furnished full protection.

TEST AREA 26 (AUGUST 12, 1935, FIG. 4)

This area was located on a 15 to 20° northeast facing slope, about 18 miles southeast of Sentinel Butte (Sec. 7, T. 138, R. 103). *Andropogon scoparius* was the dominant. The point system was not used because of the height of the vegetation. The soil type was Bainville loam (strongly rolling phase).

The abundance of *Andropogon scoparius,* and the presence in small numbers of many other species of grasses, sedges, and forbs, totaling 46 for the area and averaging 10.8 per quadrat, were associated with a fairly steep slope (15 to 20°), solum 18 inches deep, soil texture loam to silty loam, high

moisture holding capacity and usually adequate moisture below 2 feet for plant growth throughout the season; high carbonate content in all horizons, alkaline reaction throughout, and low loss-on-ignition and soluble salt content. The vegetation cover was dense so the slope was protected from excessive runoff and erosion.

TEST AREA 27 (AUGUST 15, 1935, FIG. 4)

This area was located on the lower part of a steep slope about 18 miles southeast of Sentinel Butte (Sec. 7, T. 138, R. 103). The chief dominant was big bluestem *(Andropogon furcatus)*. The soil type was Bainville fine sandy loam (rolling phase, small draw).

The dominance of *Andropogon furcatus*, the presence of *Andropogon scoparius, Bouteloua curtipendula*, Carex, and *Elymus glaucus*, the large total number (55) of species on the area and large average number (13.0) per quadrat, and the very low percentage of bare soil (2) were associated with a well developed, deep solum (36 inches), soil texture almost entirely loam becoming heavier with depth, high content of colloidal matter, high moisture holding capacity and usually available moisture for plant growth throughout the season, low content of soluble salts, calcium abundant below 3 feet, rather high loss-on-ignition, moderate carbonate content in upper 3 feet but high below, very slightly acid reaction to 20 inches, and topographic location on lower part of slope which provided additional moisture by runoff and, possibly, seepage from hill above.

TEST AREA 28 (AUGUST 2, 1935)

The steep slopes of the banks and side ravines of a narrow valley 8 miles south of Fryburg were selected as the site of this area. The chief dominant was big bluestem *(Andropogon furcatus)*. Moisture conditions appeared to be especially favorable due to seepage. Because of the height of the vegetation the point system was not used.

DESCRIPTION OF TYPICAL PROFILE IN BIG BLUESTEM TYPE IN BAINVILLE LOAM (STEEP PHASE)

Inches	
0 - 0.25	Loose, dry, dead leaves on the surface.
0.25- 1.5	Dark-brown mixture of fibrous material, roots, leaves, and old stems, mixed with mineral matter. Very light, soft and loose. Rhizomes numerous at bottom of this layer.
1.5 - 4	Dark, reddish-brown loam, small scoria particles intermixed. Breaks out into irregular pieces 1/4 to 1/2 of an inch in diameter, friable to small crumbs. Roots very numerous, rhizomes few.
4 - 9	Dark brown, clay loam. Fragmentary structure, small angular pieces hard and friable only with difficulty to fine crumbs, numerous scoria particles from 1/4 to 3/4 of an inch in length. Roots very numerous.

9	-17.5	Grayish-brown, clay to clay loam. Fragmentary structure, angular fragments range in size from 1/4 to 3/4 of an inch in diameter, friable with some difficulty to crumbs. Scoria particles numerous, occurring in horizontal layers. Roots very numerous.
17.5	-25	Grayish-brown loam, almost structureless. Scattered scoria particles are imbedded in the soil mass which is stained with occasional iron streakings. Moderate effervescence, fine roots very numerous.
25	-45	Parent material. Grayish-brown loam, grading into laminated deposits of play and sand, impervious blue clay layer 3 inches thick at 39 inches. Roots very numerous, decreasing abruptly at 32 inches, moderate effervescence. Working depth of roots 33.5 inches.

The dominance of *Andropogon furcatus,* the abundance of *Andropogon scoparius* and *Carex pennsylvanica,* the presence of prairie needle grass *(Stipa spartea)* and numerous other species of grasses and forbs making the high total number of 63 species on the area and high average number of 17.1 per quadrat were associated with loam to clay loam texture of soil, very high moisture-holding capacity and available moisture for plant growth during most of growing season, low loss-on-ignition except in surface 4 inches where it was high, acid reaction to 17.5 inches, low content of carbonates, soluble salts, and calcium, and topographic location at base of slopes where extra moisture would be received by runoff and seepage from slopes above.

TEST AREA 29 (JUNE 26, 1934)

This area was located on the lower part of a steep slope about 4 miles south of Sentinel Butte (Sec. 9, T. 139, R. 104). The crest of the hill was gravelly. The chief dominant was *Andropogon furcatus.* Soil originated, probably, from local alluvium from the slope above. The soil type was Bainville loam (steep phase).

The dominance of *Andropogon furcatus,* the moderate abundance of *Andropogon scoparius* and *Carex stenophylla,* the presence of species such as *Bouteloua curtipendula, Elymus glaucus, Aster laevis,* and *Campanula rotundifolia,* the fairly high total number of species on the area (41) and per quadrat (12.2) were associated with steep slope probably receiving additional moisture by runoff and seepage from above, sandy loam surface soil underlaid by loam, clay loam, and clay (63 percent clay content below 22 inches), alkaline reaction, extremely high colloidal content beginning at 22 inches, and dark brown solum.

TEST AREA 30 (AUGUST 5, 1935, FIG. 9)

This area was located on the lower parts of a gentle north-facing slope, near the edge of the breaks of the Little Missouri River valley about 16 miles

FIG. 9. Clumps of *Sporobolus heterolepis* forming dense stand with *Andropogon furcatus, Stipa spartea, Calamovilfa longifolia, Carex* spp., and many others, in test area 30, about 16 miles north of Kildeer. August 5, 1935.

north of Kildeer. This area was the best developed prairie type studied. It was characterized by the dominance of Sporobolus, Andropogon, Carex, Stipa, and Calamovilfa.

PROFILE DESCRIPTION OF DROPSEED-BIG BLUESTEM TYPE IN MORTON FINE SANDY LOAM (DARK PHASE)

Inches	
0 - 0.25	Decaying leaves and stems.
0.25- 1	Black sandy loam, crumb structure. Light in weight, containing much decaying vegetation, roots fairly numerous.
1 - 4	Dark brown to black, sandy loam. Light in weight, granular, readily friable, roots very numerous.
4 -11	Dark brown to black, sandy loam. Coarse, soft crumb structure, readily friable. Roots very numerous.
11 -18	Dark brown sandy loam, digs out in angular, nut-like pieces that are soft and friable. Roots very numerous.
18 -28	Brown sandy loam, blocky structure. Soil digs out in irregular chunks up to 2 inches thick, easily friable. Roots very numerous.
28 -33	Light brown sandy loam, almost structureless. Soil digs out in coarse, soft, irregular pieces that crumble easily to single grains. Roots numerous. Transitional to parent material.
33 -54	Parent material. Light brown, loose sand, strongly effervescent. Roots fairly numerous to 38 inches, almost none at 40 inches. Working depth 38 inches.

The abundance of *Sporobolus heterolepis, Carex pennsylvanica, Andropogon furcatus, Calamovilfa longifolia,* and *Stipa spartea;* the presence of certain species as *Koeleria cristata, Stipa viridula, Juncus balticus, Anemone cylindrica, Pulsatilla hirsutissima, Monarda fistulosa, Castilleja sessiliflora,* and *Lilium umbellatum;* the large number of species found in the area (86) and per quadrat (20.3); working depth of 38 inches; and the luxuriance of the vegetation (see Fig. 9) were associated with sandy loam soil on the lower portions of northerly slopes where the soil moisture received directly from precipitation would be increased by melting of snowdrifts, runoff from slopes, and, possibly, seepage. The solum was unusually dark in color for western North Dakota, extending to depth of 28 inches. The surface soil had high moisture holding capacity, loss-on-ignition, and Ca and K contents. The carbonate content was low as deep as the parent material below 33 inches. The total soluble salts were low, colloidal content moderate, and the soil was slightly acid to depth of 28 inches.

TEST AREA 31 (AUGUST 12, 1935)

This area was located about 18 miles southeast of Sentinel Butte (Sec. 8, T. 138, R. 103). It was located on a northerly slope of about 10 to 15°. The soil material originated, apparently, from hills above, now mostly eroded away. The soil type was Bainville loam (strongly rolling phase). Because of grazing on this area the vegetation was analyzed by observation only. The dominant species was *Andropogon scoparius.* In places *Carex filifolia* was abundant, in others infrequent. Other species were usually scarce. The most common were *Koeleria cristata, Calamovilfa longifolia, Agropyron smithii, Bouteloua gracilis,* and *Echinacea angustifolia.*

The dominance of *Andropogon scoparius,* the presence of species usually found in this type, and working depth 42 inches were associated with fairly shallow, poorly developed solum (17 inches deep), loam to clay loam soil with moderately high colloidal content, high percentage of carbonates and calcium beginning at the surface, soil mildly alkaline at the surface and increasing to pH 8.21 at 17 inches, low loss-on-ignition and total soluble salts.

TEST AREA 32 (JULY 27, 1935)

This area was located on the lower parts of steep slopes on the south side of a plateau on the Olstad Ranch about 15 miles southeast of Sentinel Butte (Sec. 5, T. 138, R. 103). The soil originated from material washed down from higher slopes. The soil type was Morton loam (rolling phase). Because of grazing the vegetation was studied only by observation. *Andropogon furcatus* was the dominant and *Bouteloua curtipendula* was fairly abundant. Some of the other species were *Agropyron smithii, Panicum virgatum, Stipa viridula, Koeleria cristata, Andropogon scoparius, Artemisia gnaphalodes, Achillea lanulosa,* and *Symphoricarpos occidentalis.*

The dominance of *Andropogon furcatus*, the presence of other characteristic species listed above, and the high density of the vegetation were associated with the physiographic location (base of steep slopes) where moisture is received by runoff from above, from melting snowdrifts and probably by seepage; soil texture chiefly sandy loam; dark colored, well developed solum to depth of at least 25.5 inches; high water-holding capacity, high loss-on-ignition in 1 to 3-inch layer, low carbonate content to depth of 40 inches, slightly acid reaction to depth of 32 inches, and small quantities of soluble salts throughout.

TEST AREA 33 (AUGUST 8, 1935)

This area was located on lower slopes and in bottoms of small draws or swales in a valley, not subject to overflow, about 8 miles west of Dickinson. The frequency-abundance and point methods were not used because the area was grazed. *Buchloe dactyloides* was dominant and *Agropyron smithii* was abundant. Other species occurring infrequently were *Bouteloua gracilis*, *Stipa viridula*, *Poa buckleyana*, and *Carex stenophylla*.

DESCRIPTION OF PROFILE IN BUFFALO GRASS TYPE IN GRAIL SILTY CLAY LOAM

Inches	
0 - 1	Grayish-brown clay. Soft, friable crumb structure, somewhat platy. Roots numerous, rhizomes frequent.
1 - 7	Dark-brown to black clay. Poorly defined prismatic structure, vertically elongated chunks break into small, hard, angular fragments about 1/4 to 3/4 inch thick. Roots very numerous.
7 -13.5	Brown clay. Poorly defined prismatic structure, prisms break into hard angular fragments. Effervescence moderate, roots numerous.
13.5-25	Light-brown clay. Angular fragmentary structure, friable only with difficulty. Violent effervescence, white flecks and streaks numerous. Black layer, 1 inch thick, at bottom of this horizon did not effervesce. Roots numerous.
25 -32	Light brown, sandy clay loam, almost structureless. Digs out in irregular, hard, angular pieces. Effervescence occurs only in occasional pockets, white streakings few, roots frequent.
32 -42	Brown, compact clay with occasional white streaks. Effervescence moderate to strong, roots infrequent. Working depth 33 inches.

The dominance of Buchloe, the abundance of *Agropyron smithii*, and the presence of other species as *Bouteloua gracilis* and Poa, were associated with soil containing a high proportion of clay and much colloidal matter, high soluble salt content especially below 32 inches, slightly alkaline soil reaction, low loss-on-ignition, fairly low carbonate content, and unusually strong effervescence in the 13.5 to 25-inch layer which was marked by numerous white streaks and flecks.

TEST AREA 34 (AUGUST 7, 1935, SEE FIG. 10)

This area was located on a fairly high level area between hills about 10 miles northwest of Kildeer along N. D. Highway No. 22. Examination of

FIG. 10. View of soil profile, similar to that in test area 34, showing solodized solonetz structure on Morton Loam, solonized phase, near Grassy Butte. "The caps of the columns are slightly exposed in the picture, that is, there is a little shelf at that point. The soil above the column shows some relicts of an old prismatic structure but when removed they are very friable. In places this soil shows a definite platy structure. The upper 4 or 5 inches of the columns is very dark brown clay, very hard when dry, and breaks into angular small nut-size pieces that are nearly cubical. The picture shows the mottling of white in the lime zone beginning at about 23 inches. The cover on the uneroded soil was largely grama grass." Photograph and description by Charles E. Kellogg, Chief, U. S. Soil Survey.

the vegetation showed that *Boutcloua gracilis* was the chief dominant. *Poa buckleyana* occurred frequently. *Agropyron smithii, Stipa viridula,* and *Stipa comata* were scarce. The soil type was Patent silty clay loam.

The dominance of *Bouteloua gracilis* in mixture with *Poa buckleyana* and a few other grasses was associated with soil containing a high percentage of clay (24.5 to 36.7 percent); high colloid and calcium contents, fairly high concentration of soluble salts below 30.5 inches, no effervescence above 23 inches but strong below 37.5 inches, well developed solum to depth of about 23 inches, slightly acid reaction to 23 inches, and low loss-on-ignition.

TEST AREA 35 (AUGUST 7, 1935, FIG. 11)

This area was located on a flat area between low hills about 3 miles northwest of Kildeer along N. D. Highway No. 22. The chief dominants were *Distichlis spicata* and *Puccinellia nuttalliana. Agropyron smithii* was also

FIG. 11. *Puccinellia airoides* in mixture with *Distichlis spicata* and some *Agropyron smithii*, as in area 35, saltgrass-alkali meadowgrass type. About 16 miles north of Kildeer. August 5, 1935.

abundant. Other characteristic species were *Plantago elongata, Atriplex argentea, Dondia depressa,* and *Opuntia fragilis.*

DESCRIPTION OF PROFILE IN SALTGRASS TYPE IN PATENT CLAY LOAM (STRONGLY SOLONIZED PHASE)

Inches	
0 - 1.5	Light gray, fine sandy loam. Somewhat platy structure, vesicular, brittle, pulverizes easily to fine crumbs. Roots few.
1.5- 4	Grayish brown loam. Columnar structure, columns very hard, rounded caps fairly well developed. Roots very numerous, rhizomes numerous.
4 - 8	Grayish-brown clay. Prismatic structure, prisms about 2 inches in diameter, very hard. Effervescence moderate, roots numerous, rhizomes frequent.
8 -14	Grayish-brown silt loam. Prismatic structure less well developed than in layer above. Effervescence moderate, roots frequent.
14 -19	Brown clay, poorly defined prismatic structure, effervescence moderate, roots frequent.
19 -37	Brown clay, with some white mottlings. Massive, dry pieces very hard. Effervescence moderate, roots infrequent.
37 -42	Parent material. Yellowish brown clay, effervescence moderate, roots infrequent to scarce. Working depth of roots 26 inches.

The dominance and abundance of Distichlis, Puccinellia, and *Agropyron smithii,* and the presence of Dondia, Atriplex, Opuntia, and Plantago were associated with unusually high concentration of soluble salts below 1.5 inches, reaching 13,900 p.p.m. in the 8 to 14-inch layer, unusually high concentration of sodium throughout the profile, potassium content high to depth of 19 inches, high percentage of clay and colloids in most of the horizons, fairly high alkaline reaction between 4 and 19 inches, low loss-on-ignition, moderately large amount of carbonates below 8 inches, and shallow solum of about 14 inches.

TEST AREA 36 (AUGUST 7, 1935)

This area was located on a gently sloping upland about 5 miles northwest of Kildeer along N. D. Highway No. 22. Dominants were *Bouteloua gracilis* and *Stipa comata. Carex stenophylla* and *C. pennsylvanica* were difficult to distinguish and together rated as abundant. Other important species were *Agropyron smithii, Calamagrostis montanensis, Carex filifolia, Malvastrum coccineum,* and *Collomia linearis.* The soil type was Morton sandy loam.

The dominance of Bouteloua, Stipa, and Carex, the presence of numerous other species, and the deep working level of 51 inches were associated with chiefly sandy loam texture, moderately low colloidal content, low loss-on-ignition, carbonates and soluble salts, acid reaction to depth of 38.5 inches, fairly high calcium content, fairly high water-holding capacity for soil containing such high percentage of sand, and a fairly well developed solum to depth of about 38 inches.

CLASSIFICATION OF TEST AREAS INTO TYPES

Chiefly on the basis of vegetation and topography the test areas included in this paper have been classified into 9 major types. These types have been named according to the chief species in each, which are shown comparatively in Figure 12. Weaver and Fitzpatrick (1934) classified 135 areas of tallgrass prairie into 6 types, 2 of which were climax.

1. *The grama-needlegrass-sedge type* (Figs. 2, 3). Test areas 1, 2, 3, 4, 6, 7, and 36 appear to have sufficient resemblance, especially in species and topography, to be classified in this type. The topography varies from upland plateaus to gentle upland slopes (see Figs. 2, 3). Since the soil has been free from excessive erosion and deposition for a long period, it is usually mature. The vegetation, where protected from excessive grazing, mowing, or other use, has apparently reached stabilization as far as this is possible under the severe climatic fluctuations. In years of favorable rainfall, the cover is fairly dense.

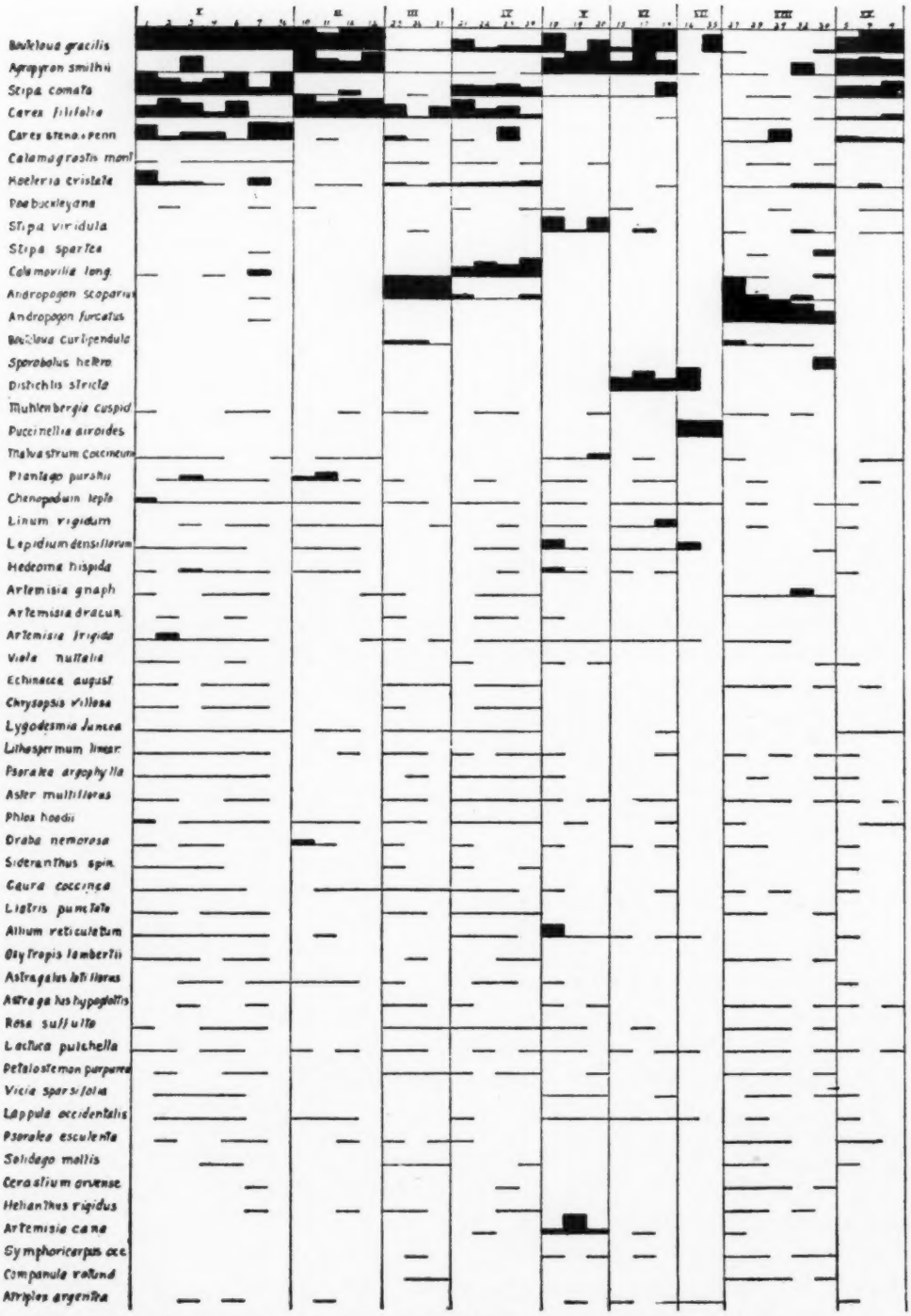

FIG. 12. The importance of 57 of the leading species is shown comparatively for test areas and types. Each species is given 10 small horizontal spaces. Each small vertical space has a F x A value of 10. In area 1 *Bouteloua gracilis* occupies 10 horizontal spaces so it has an F x A value of 100, but in area 11 it has a F x A value of 75 so it occupies 7.5 vertical spaces. *Bouteloua gracilis* is absent on 5 areas. Most of the species have such low F x A values that lines alone are used to indicate their presence.

TABLE 3. Characteristics of soils according to horizons described in soil profile descriptions for each type.

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 1. Bouteloua, Stipa, Carex.																
1 — 7	74.0	13.7	12.3	12.1	16.8	49.6	4.92	6.46	1.9	557	2	2,000	25+	0	400	0
7 —17	76.8	13.9	9.3	12.0	16.3	44.3	3.00	6.65	2.3	680	0	3,000	25+	0	150	0
17 —20.5	77.7	13.2	9.1	18.8	15.5	44.8	3.36	7.80	2.6	484	0	3,000	25+	0	150—	0
20.5—32	76.3	14.2	9.5	12.6	17.1	45.3	4.80	8.09	7.5	424	0	3,000	50	0	150—	0
32 —40	76.7	13.4	9.8	11.6	16.7	44.0	3.47	8.02	14.8	544	0	3,000	25	0	150—	0
Ave. to W.D. 40 in.	76.3	13.8	9.9	12.6	16.7											
TEST AREA 2. Bouteloua, Carex, Stipa.																
1 — 5.5	71.8	20.4	7.8	6.6	11.9	55.9	5.68	6.75	2.2	473	0	2,000	10—	0	600	0
5.5—13	71.5	18.2	10.3	8.3	13.1	50.9	4.77	7.43	1.7	398	0	2,000	10—	0	500	0
13 —23	60.0	26.0	14.0	10.3	18.0	52.9	3.70	7.70	3.1	476	0	2,000	T	0	200	0
23 —31	55.7	26.0	18.3	16.6	22.0	57.9	5.31	7.97	4.8	473	0	2,000	0	0	150	0
31 —42	52.9	27.9	19.2	16.4	24.6	52.8	7.27	8.04	8.7	600	0	1,000	0	0	150—	0
Ave. to W.D. 36 in.	62.0	23.9	14.1	11.7	18.0											
TEST AREA 3. Bouteloua, Agropyron, Carex, Stipa.																
1 — 4	31.4	43.5	25.1	22.8	31.8	64.0	6.47	6.01	6.1	577	T	1,000	100	0	200	T
4 — 9	32.5	38.3	29.2	25.8	33.3	58.1	5.08	5.92	7.8	480	T	1,000	100	0	150	T
9 —14	31.6	40.6	27.8	25.8	34.3	60.9	4.71	6.35	8.7	414	T	2,000	100+	0	T	T
14 —24	28.7	39.0	32.3	28.5	38.9	58.2	6.20	8.11	24.2	553	T	3,000	50	0	T	0
Ave. to W.D. 24 in.	30.5	39.8	29.7	26.6	35.7											
TEST AREA 4. Bouteloua, Stipa, Carex.																
0.5— 2.5	63.1	22.6	14.3	11.7	19.7	54.9	6.22	5.78	8.3	334	T	2,000	100	0	400	T
2.5— 6	63.9	20.9	15.2	11.9	20.0	55.2	4.47	5.82	7.7	359	T	2,000	100	0	200	0
6 —15	62.7	17.8	19.5	17.3	23.7	48.9	3.77	6.38	8.6	324	T	2,000	50	0	150	0
15 —22.5	64.3	16.7	19.0	16.0	22.9	49.6	3.46	6.45	6.4	551	T	2,000	50	0	T	0
22.5—33	64.9	14.2	20.9	18.8	24.4	51.7	3.46	6.82	7.9	382	T	1,000	100	0	T	0
33 —43	70.9	10.3	18.8	17.9	21.4	50.7	2.95	7.18	4.6	390	T	1,000	100	0	T	0
43 —50.5	76.4	4.5	19.1	16.8	20.8	42.1	2.60	7.56	3.9	411	2	3,000	200	0	T	0
Ave. to W.D. 40 in.	63.8	17.5	18.7	16.6	22.9											
TEST AREA 5. Bouteloua, Agropyron, Stipa, Carex.																
0 — 2	55.0	31.5	13.5	9.7	19.1	55.0	6.77	7.04	7.7	428	0	2,000	50	0	600	0
2 — 7	54.7	27.4	17.9	15.5	23.8	53.7	6.45	6.85	8.3	476	0	2,000	10	T	150	0
7 —21	32.9	40.3	26.8	23.4	33.2	50.8	6.72	8.21	17.0	419	0	1,000	10	T	150	0
21 —30	52.2	25.7	22.1	18.8	27.6	50.0	6.30	8.38	15.6	499	0	1,000	10	T	150	T
30 —33	33.8	34.4	31.8	23.0	39.5	54.7	5.29	8.06	15.7	3,250	0	2,000	10	T	150	8
33 —38	16.9	50.0	33.1	8.6	57.3	66.9	10.60	7.53	16.6	5,500	0	2,000	10	1,000	150	8
38 —59	30.8	45.8	23.4	9.4	38.1	56.8	8.62	7.62	20.8	6,300	0	2,000	25	1,000	150	8
Ave. to W.D. 28 in.	43.3	33.6	23.1	21.9	29.1											
TEST AREA 6. Bouteloua, Stipa, Carex.																
1 — 3.5	70.2	18.8	11.0	8.3	14.2	54.8	5.09	5.79	7.8	375	0	1,000	10	0	200	0
3.5—13	73.9	13.7	12.4	10.6	14.9	61.7	3.61	5.92	7.9	379	0	1,000	10	0	200	0
13 —22	81.8	9.0	9.2	7.9	12.6	47.3	2.84	6.92	7.4	383	0	1,000	10	0	150—	0
22 —34	82.8	5.8	11.4	8.7	13.2	45.3	2.97	8.02	10.6	454	0	1,000	10	0	T	0
34 —44	87.0	5.5	7.5	6.3	8.5	39.4	1.71	8.21	10.9	451	0	1,000	25	0	150—	0
Ave. to W.D.29.5 in.	78.4	10.6	11.0	9.1	13.7											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 7. Bouteloua, Carex, Koeleria, Calamovilfa, Stipa.																
1.5— 3	58.2	27.5	14.3	11.7	19.7	64.8	6.77	6.18	7.8	360	0	2,000	50	0	200	0
3 — 7.5	57.3	26.0	16.7	14.1	23.1	62.8	5.99	6.18	8.3	408	0	1,000	25—	0	T	0
7.5—18	65.6	18.0	16.4	13.6	19.6	53.4	4.04	6.43	7.8	514	0	1,000	25	T	T	0
18 —27	71.7	14.2	14.1	12.9	16.8	49.4	3.16	6.84	8.3	439	2	1,000	50	0	T	0
27 —38	70.2	14.0	15.8	14.3	18.6	45.3	3.15	7.11	7.9	318	0	750	25	0	T	0
38 —44	76.3	11.3	12.4	10.6	15.0	42.6	3.60	8.11	7.6	281	0	2,000	50	0	T	T
44 —60	87.0	6.2	6.8	5.7	8.9	38.7	2.13	8.38	7.2	283	0	1,000	25	0	T	0
Ave. to W.D. 33 in.	66.7	17.8	15.5	13.5	19.0											
TEST AREA 8. Bouteloua, Agropyron, Stipa.																
1 —10	18.7	32.6	48.7	42.7	59.4			6.80								
10 —18	21.8	31.3	46.9	41.6	56.0			7.75								
18 —34	21.7	33.2	45.1	39.0	55.7			8.02								
34 —53	35.8	27.0	37.2	32.8	45.1			8.31								
53 —66	73.9	14.4	11.7	11.2	13.8			8.50								
Ave. to W.D. 34 in.	20.9	32.6	46.5	32.5	44.8											
TEST AREA 10. Agropyron, Bouteloua, Carex.																
1 — 4.5	34.8	41.3	23.9	20.2	33.3	60.5	7.8	7.36	7.4	692	T	2,000	17	0	150	0
4.5—10.5	37.3	32.2	30.5	26.7	38.8	60.7	10.6	7.87	25.9	626	0	2,000	10—	0	150	0
10.5—27	29.7	35.0	35.3	29.5	40.3	51.9	9.5	8.38	31.4	634	0	2,000	10—	0	150—	0
27 —45	33.5	29.8	36.8	17.2	43.8	39.8	17.7	8.63	31.2	236	0	2,000	10—	2,000	150—	T
Ave. to W.D. 25 in.	32.4	35.2	32.4	22.5	38.9											
TEST AREA 11. Agropyron, Bouteloua, Carex.																
0 — 1.5	32.6	49.8	17.6	15.3	29.0	84.7	11.6	7.20	8.3	626	20	2,000	50	T	600	0
1.5— 3.5	30.1	44.9	25.0	18.3	33.7	68.8	8.1	7.30	8.3	520	2	3,000	25	T	600	0
3.5— 7.5	38.4	38.0	23.6	18.4	30.9	57.1	4.9	7.50	11.0	604	0	2,000	25	0	150	0
7.5—14	20.6	44.7	34.7	30.1	46.7	61.0	7.2	7.70	8.9	648	0	2,000	25	T	150—	T
14 —26	23.7	40.5	35.8	30.8	45.1	63.0	4.7	7.80	14.0	553	0	3,000	10	0	150	0
26 —47.5	39.5	33.8	26.7	24.2	32.4	53.1	4.0	7.90	19.2	559	0	3,000	10	0	150—	T
47.5—62	46.4	30.7	22.9	19.7	26.9	48.0	2.6	8.00	15.0	1,538	0	2,000	0	0	150—	T
Ave. to W.D. 35 in.	29.6	39.9	30.5	25.2	38.2											
TEST AREA 12. Bouteloua, Agropyron, Carex.																
0.5— 2	62.0	25.8	12.2	9.8	16.1	60.0	6.9	6.8	8.6	492	T	1,000	50	0	150	0
2 — 6	46.5	31.1	22.4	19.4	28.7	59.2	6.7	6.6	7.2	608	T	750+	50	0	T	0
6 —10	44.0	32.6	23.4	19.8	30.9	54.8	7.1	8.2	17.3	596	T	750	50	0	T	0
10 —20	39.7	31.8	28.5	25.2	37.2	54.2	6.0	8.3	22.0	566	T	750+	50	T	T	T
20 —27	25.1	36.4	38.5	32.5	46.2	57.5	10.2	8.4	19.9	568	T	750	100	T	T	T
27 —40	29.1	38.3	32.6	29.0	41.3	54.4	6.9	8.4	22.7	618	T	750	50	T	T	T
Ave. to W.D. 32 in.	37.2	33.6	29.2	24.9	36.4											
TEST AREA 13. Bouteloua, Agropyron, Carex.																
1.5—15	32.5	37.3	30.2	25.9	28.2			7.5								
15 —21	29.4	37.2	33.4	28.4	44.1			7.8								
21 —37	30.0	40.9	29.1	25.1	37.9			8.0								
37 —50	33.6	40.3	26.1	18.7	35.1			8.2								
Ave. to W.D. 28 in.	31.1	38.3	30.6	24.8	37.4											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 14. Bouteloua, Agropyron, Stipa, Distichlis.																
0 — 1	56.9	24.9	18.2	15.9	24.0	56.7	7.1	7.28	20.1	592	T	2,000	50	T	200	0
1 — 3	60.6	25.3	14.1	14.2	21.3	53.9	6.0	7.18	18.2	463	T	2,000	25	T	150	0
3 — 7	66.9	15.0	18.1	15.6	21.5	47.5	3.9	7.70	18.3	470	0	2,000	25	0	200	0
7 — 8.5	65.7	16.5	17.8	14.3	22.2	51.3	3.3	7.77	16.4	592	0	1,000	10	0	200	0
8.5—15.5	65.6	20.2	14.2	11.0	17.0	26.8	4.9	8.00	16.9	1,276	0	2,000	25	T	400	0
15.5—40	60.3	23.0	16.7	15.1	20.0	49.1	2.9	8.40	17.0	5,200	0	2,000	10	1,500	300	T
40 —49	Coarse scoria in heavy clay					53.6	3.0	8.60	16.5	4,600	0	1,000	10	1,500	150	T
49 —54	52.5	28.7	18.8	16.6	22.5	52.0	4.1	8.70	23.1	3,500	0	2,000	25	1,500	150—	8
Ave. to W.D. 26 in.	62.9	20.9	16.2	14.5	20.5											
TEST AREA 15. Agropyron, Distichlis.																
0 — 3	38.9	44.7	16.4	13.1	26.9	59.3	10.2	7.50	18.0	915	10	4,000	50	0	200	T
3 — 4	30.3	42.0	27.7	12.2	29.3	86.9	12.4	7.60	12.1	746	2	3,000	50	0	400	T
4 — 6	26.1	57.4	16.5	12.8	30.5	67.1	7.0	7.60	16.8	749	T	3,000	25	0	150	T
6 —11.5	26.2	56.3	17.5	13.8	29.8	61.8	9.7	7.70	19.8	3,550	T	2,000	25	T	150—	T
11.5—20.5	27.6	56.5	15.9	12.5	27.7	61.4	7.2	7.80	19.4	4,800	T	2,000	25	150	T	T
20.5—51	39.8	40.7	19.5	15.5	27.7	55.8	4.5	8.30	18.0	4,800	T	2,000	25	150	T	T
Ave. to W.D. 22 in.	29.5	53.2	17.3	13.4	28.4											
TEST AREA 16. Distichlis, Puccinellia.																
0 — 4.5	41.3	40.8	17.9	14.4	27.0	58.2	4.8	7.70	17.6	1,587	0	3,000	25	T	T	0
4.5—15.5	22.5	53.2	24.3	17.4	28.3	59.3	6.6	8.10	18.6	11,100	2	3,000	25	200	T	0
15.5—35.5	21.5	48.8	29.7	25.3	40.7	60.6	7.0	8.20	21.5	8,500	T	3,000	25	200—	0	0
35.5—54	32.6	43.4	25.0	22.1	33.2	55.3	4.8	8.30	21.5	4,300	T	3,000	50	200	T	0
Ave. to W.D. 18 in.	27.0	49.5	23.5	15.5	35.8											
TEST AREA 17. Agropyron, Distichlis, Bouteloua.																
0 — 2	57.0	28.7	14.3	11.9	19.6	47.4	6.6	7.16	14.5	603	0	2,000	0	0	600	0
2 — 6	52.1	32.1	15.8	13.2	22.9	46.6	5.0	7.28	15.6	660	0	1,000	0	0	600	0
6 —20	48.0	35.4	16.6	14.1	22.6	48.2	5.6	7.53	16.0	875	0	1,000	0	0	150—	0
20 —31	38.9	44.1	17.0	16.4	30.0	52.8	7.2	7.90	14.0	4,800	0	2,000	0	1,500	150	0
31 —66	57.0	25.7	17.3	10.3	21.9	44.3	3.7	8.00	16.9	7,200	0	2,000	0	1,500	150—	0
Ave. to W.D. 39 in.	48.2	35.1	16.7	13.8	24.4											
TEST AREA 18. Artemisia cana, Bouteloua, Agropyron, Stipa viridula.																
0 — 2	23.1	46.9	30.0	21.9	42.2	68.5	13.4	7.60	9.7	637	0	3,000	50	0	600	T
2 — 7	15.0	46.7	38.3	30.0	50.7	71.9	11.1	7.70	8.7	595	0	3,000	50	0	200	0
7 —11	12.9	43.8	43.3	36.6	60.2	69.8	12.8	7.70	8.8	870	0	3,000	25	T	150—	0
11 —18	16.2	48.2	35.6	28.8	50.3	61.0	6.6	7.70	13.5	688	0	2,000	25	0	150—	0
18 —27	20.1	47.2	32.7	27.5	44.3	56.9	8.3	7.70	15.2	537	0	2,000	10	0	150—	0
27 —61	16.6	46.1	37.3	32.3	49.4	60.6	6.6	7.70	16.0	910	0	2,000	10	0	150—	0
Ave. to W.D. 31 in.	17.1	46.8	36.1	29.0	49.2											
TEST AREA 19. Artemisia cana, Agropyron.																
0.5—12.5	37.0	50.6	12.4	11.4	21.2	44.9	5.4	7.70	15.9	812	0	2,000	0	T	150—	0
12.5—48.5	12.2	64.2	23.6	8.7	43.2	54.5	3.5	7.70	15.9	1,284	0	1,000	0	T	150—	0
48.5—53	63.3	28.1	8.6	7.7	12.4	40.4	7.4	7.26	14.3	1,050	2	2,000	0	1,000	150	T
53 —64	36.6	49.7	13.7	12.3	18.0	47.5	2.4	7.94	17.6	1,220	20	1,000	0	1,000	150	0
Ave. to W.D. 52 in.	21.4	58.6	20.0	9.4	36.2											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 20. Artemisia cana, Agropyron, Stipa viridula, Bouteloua.																
2.5—10	15.6	25.8	58.6	51.9	69.7	.....	.....	7.53	....	.....	....	.....	.....	.....	.....	..
10 —18.5	21.2	39.5	39.3	33.3	51.9	.....	.....	8.13	....	.....	....	.....	.....	.....	.....	..
18.5—25.5	16.3	62.3	21.4	16.4	29.6	.....	.....	7.86	....	.....	....	.....	.....	.....	.....	..
25.5—40.5	78.2	14.8	7.0	6.5	9.7	.....	.....	8.23	....	.....	....	.....	.....	.....	.....	..
Ave. to W.D. 42 in.	41.7	30.9	27.4	23.5	35.8											
TEST AREA 21. Calamovilfa.																
0 — 6	87.3	9.4	3.3	3.1	5.1	40.9	3.4	7.50	15.2	378	0	1,000	25	0	T	0
6 —74	76.0	16.3	7.7	5.9	10.9	41.5	2.6	7.70	16.1	494	T	2,000	25	0	T	0
Ave. to W.D. 70 in.	77.0	15.7	7.3	5.7	10.4											
TEST AREA 22. Calamovilfa, Carex.																
1.5— 3.5	76.7	16.2	7.1	5.5	11.1	51.8	4.1	6.11	6.5	377	0	1,000	50	0	600	0
3.5— 8.5	79.9	12.8	7.3	6.8	12.2	48.1	3.2	6.28	6.8	370	0	1,000	25	0	600	0
8.5—13	78.3	9.8	11.9	8.6	15.9	45.8	2.5	6.26	6.2	374	0	1,000	25	0	600	0
13 —19	78.3	13.3	8.4	7.0	12.5	43.8	2.6	6.43	7.2	327	0	1,000	25	0	150	0
19 —24	79.8	8.5	11.7	9.2	13.0	43.8	2.1	6.52	6.7	364	0	1,000	10	0	150	0
24 —69	78.8	12.2	9.0	8.0	11.8	44.3	2.4	6.52	6.0	569	0	1,000	10	0	150	T
Ave. to W.D. 56 in.	78.7	12.1	9.2	7.8	12.3											
TEST AREA 23. Calamovilfa, Carex, Stipa.																
0 — 3	76.4	15.0	8.6	6.5	12.4	52.3	4.5	6.31	7.5	284	0	1,000	25	0	500	0
3 — 8	73.6	13.7	12.7	9.7	15.6	48.7	3.8	6.18	5.9	327	0	1,000	10	0	150	0
8 —17.5	71.7	15.1	13.2	12.4	16.9	52.4	3.0	6.48	6.8	436	0	750	10	0	T	0
17.5—26.5	69.2	16.6	14.2	12.1	18.2	52.6	2.4	6.50	7.0	391	0	1,000	10	0	150	0
26.5—42	66.4	17.1	16.5	15.0	20.6	51.7	2.4	6.85	4.2	588	0	750	10	0	150	0
42 —60	60.2	21.0	18.8	16.8	23.4	52.1	3.1	7.34	6.2	252	0	1,000	10	0	T	0
Ave. to W.D. 57 in.	67.3	17.3	15.4	13.7	19.5											
TEST AREA 24. Calamovilfa, Carex.																
1.5—23	69.3	16.6	14.1	12.1	18.9	.....	.....	6.48	....	.....	....	.....	.....	.....	.....	..
23 —39	74.4	13.9	11.7	10.1	14.4	.....	.....	6.50	....	.....	....	.....	.....	.....	.....	..
39 —61	74.0	11.9	14.1	11.8	16.5	.....	.....	7.04	....	.....	....	.....	.....	.....	.....	..
61 —72	77.7	9.4	12.9	11.5	14.7	.....	.....	7.47	....	.....	....	.....	.....	.....	.....	..
Ave. to W.D. 58 in.	72.4	14.3	13.3	11.2	16.4											
TEST AREA 25. Andropogon scoparius.																
0 — 1.5	66.9	27.1	6.0	4.6	9.3	52.5	6.22	7.20	7.1	406	2	1,000	25	0	T	0
1.5 — 4	50.3	36.4	13.3	13.5	22.4	64.7	8.10	7.40	21.7	463	T	2,000	25	0	T	0
4 — 7	22.7	53.6	23.7	17.0	33.5	64.3	8.17	7.60	23.8	672	0	3,000	25	0	0	0
7 —12	9.0	54.8	36.2	29.8	54.5	63.4	8.26	7.70	30.0	506	0	2,000	25	0	T	0
12 —20	25.0	59.2	15.8	12.8	26.0	54.2	7.10	7.80	26.0	517	0	3,000	10	T	150	0
20 —37	30.5	60.8	8.7	6.6	16.4	53.2	1.90	7.90	25.9	312	0	3,000	10	T	T	0
37 —53	18.0	71.9	10.1	7.5	21.5	52.3	5.52	7.90	28.5	629	0	2,000	25	0	T	0
Ave. to W.D. 26 in.	28.0	54.0	18.0	13.7	28.8											
TEST AREA 26. Andropogon scoparius.																
1 — 5	24.8	56.9	18.3	15.5	30.5	68.2	8.53	7.40	19.6	630	T	2,000	25	0	T	T
5 — 9.5	16.9	54.8	28.3	23.9	40.1	64.3	8.40	7.70	23.5	743	T	3,000	25	0	T	0
9.5—18	17.7	52.2	30.1	23.8	42.1	61.8	5.15	7.90	22.9	559	T	2,000	25	0	T	0
18 —23.5	40.1	40.5	19.4	16.2	27.4	58.8	4.68	8.20	22.4	387	T	2,000	25	0	T	0
23.5—53	26.9	47.6	25.5	19.5	34.0	55.7	4.50	8.40	26.1	584	T	2,000	25	0	0	0
Ave. to W.D. 48 in.	25.6	49.1	25.3	19.9	35.0											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 27. Andropogon furcatus.																
0 — 3	50.0	41.5	8.5	7.1	13.8	72.5	10.15	6.94	13.3	566	2	1,000	50	0	T	0
3 — 6	46.7	39.6	13.7	12.2	20.6	76.6	8.70	6.87	11.8	541	2	1,000	50	0	0	0
6 —12	43.3	42.1	14.6	12.1	21.5	71.9	8.78	6.72	11.7	642	T	1,000	50	0	0	T
12 —20	45.9	40.1	14.0	11.6	19.7	62.3	7.68	7.01	10.3	543	0	2,000	50	0	0	0
20 —36	46.1	38.1	15.8	12.7	21.9	63.6	8.28	7.29	8.2	377	0	2,000	50	0	0	0
36 —41	44.9	34.7	20.4	17.5	27.6	56.2	9.60	8.00	17.9	364	T	3,000	25	0	0	0
41 —48	49.9	30.1	20.0	17.6	26.1	52.0	8.98	8.20	20.1	548	T	3,000	25	0	0	T
Ave. to W.D. 46 in.	46.2	38.1	15.7	13.1	21.9											
TEST AREA 28. Andropogon furcatus.																
1.5— 4	44.6	36.2	19.2	15.5	26.6	99.6	13.65	5.50	8.4	496	0	1,000	25	0	150	0
4 — 9	31.7	40.8	27.5	23.2	34.7	72.9	7.61	5.84	9.3	678	0	1,000	25	0	200	0
9 —13	30.9	35.8	33.3	29.8	42.3	72.3	6.16	5.99	8.4	670	0	1,000	10	0	150—	0
13 —17.5	43.6	31.0	25.4	21.6	32.5	65.1	5.27	6.28	9.0	612	0	750	25	T	150—	0
17.5—25	45.5	37.6	16.9	14.0	21.6	57.1	4.31	7.11	12.8	509	0	1,000	T	0	T	0
25 —39	41.9	45.2	12.9	10.8	18.3	59.6	4.02	7.24	17.0	622	0	750	10	T	T	0
Ave. to W.D. 33.5in.	40.6	38.5	20.9	17.8	27.2											
TEST AREA 29. Andropogon furcatus.																
1 — 4	55.7	29.0	15.3	13.1	21.1	.....	.....	7.41	....	.....	....	.....	.....	.....	.....	..
4 —15	49.2	36.1	14.7	11.9	22.7	.....	.....	7.73	....	.....	....	.....	.....	.....	.....	..
15 —22	32.6	42.2	25.2	19.1	34.8	.....	.....	8.00	....	.....	....	.....	.....	.....	.....	..
22 —41	6.7	30.3	63.0	53.1	79.1	.....	.....	8.03	....	.....	....	.....	.....	.....	.....	..
Ave. to W.D. 41 in.	25.9	35.5	38.6	32.0	50.2											
TEST AREA 30. Sporobolus, Andropogon.																
1 — 4	61.7	34.4	3.9	2.8	8.2	91.6	12.20	6.35	5.5	406	0	2,000	25	0	600	0
4 —11	65.1	26.4	8.5	7.0	15.0	60.4	5.80	6.60	5.7	369	0	2,000	25	T	600	0
11 —18	69.5	23.6	6.9	5.1	13.0	57.3	5.10	6.67	5.5	377	0	2,000	25—	0	600	0
18 —28	71.2	18.0	10.8	8.0	15.7	54.3	3.63	6.60	7.3	275	0	1,000	10	T	300	0
28 —33	76.2	12.3	11.5	8.9	15.2	51.2	3.80	7.50	8.6	322	0	1,000	10	T	150—	0
33 —54	75.9	10.3	13.8	11.8	17.5	48.7	3.70	8.00	18.1	374	0	2,000	10—	T	150—	0
Ave. to W.D. 38 in.	70.2	20.2	9.6	7.7	14.6											
TEST AREA 31. Andropogon scoparius.																
1.5— 4.5	43.3	37.1	19.6	16.5	26.0	63.9	6.87	7.53	21.1	572	T	3,000	50	0	T	0
4.5—12	45.2	39.0	15.8	13.2	22.0	62.5	6.50	7.89	25.1	622	T	3,000	25	0	T	0
12 —17	29.1	43.2	27.7	21.1	36.4	59.4	8.03	8.11	30.9	566	60	3,000	25	0	T	0
17 —23	28.6	47.1	24.3	19.8	33.5	57.8	7.90	8.21	30.1	444	40	3,000	25+	T	T	0
23 —45	31.5	43.5	25.0	19.9	32.8	51.6	6.10	8.12	30.9	570	10	3,000	50+	0	T	0
Ave. to W.D. 42 in.	34.2	42.7	23.1	18.0	30.1											
TEST AREA 32. Andropogon furcatus.																
1 — 3	31.5	54.2	14.3	12.4	24.7	89.0	11.60	6.41	7.4	430	0	1,000	25	0	150	0
3 —10	52.5	36.1	11.4	8.6	16.7	74.9	6.57	6.52	7.2	329	0	1,000	25	0	150—	0
10 —21	47.7	39.6	12.7	8.8	18.9	73.7	7.59	6.52	6.4	492	0	1,000	10	0	150—	0
21 —25.5	50.5	32.0	17.5	14.6	24.1	62.2	4.55	6.67	6.7	492	0	1,000	25	0	150—	0
25.5—32	56.2	29.4	14.4	11.9	19.6	56.6	4.69	6.87	10.2	436	0	1,000	10	0	150—	0
32 —40	46.1	36.6	17.3	14.6	24.2	62.2	5.57	7.80	9.0	401	0	1,000	25	0	150—	0
40 —46	50.2	34.5	15.3	12.6	21.5	57.9	4.26	7.97	15.1	332	0	1,000	10	0	T	0
46 —49	50.2	25.4	24.4	20.7	30.8	59.0	5.95	8.38	27.8	443	0	750	10	0	T	0
Ave. to W.D. 36 in.	49.5	36.5	14.0	10.9	20.2											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts. P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 33. Buchloe.																
1 — 7	22.4	34.8	42.8	35.4	54.2	60.3	5.87	7.40	6.3	1,032	0	1,000	25-	0	150	0
7 —13.5	15.1	40.3	44.6	37.7	60.9	57.2	6.40	7.80	9.0	1,332	0	2,000	25	0	150—	0
13.5—25	17.0	32.8	50.2	42.1	62.2	57.3	6.22	7.70	9.5	1,184	T	2,000	50	0	T	0
25 —32	63.6	11.2	25.2	22.0	29.3	46.8	2.95	7.70	7.2	62.	0	750	25	T	150—	0
32 —42	41.8	20.9	37.3	31.6	45.4	57.3	4.30	7.80	7.7	2,456	0	1,000	50	T	T	0
Ave. to W.D. 33 in.	28.6	29.6	41.8													
TEST AREA 34. Bouteloua, Poa buckleyana.																
1.5— 7	32.2	43.3	24.5	17.9	34.3	60.1	7.87	6.41	5.8	392	T	5,000	10	0	200	0
7 —14	25.6	37.7	36.7	21.3	47.6	59.5	6.10	6.67	6.7	840	0	2,000	10+	0	T	0
14 —23	19.2	47.6	33.2	28.2	45.9	59.3	5.82	6.79	7.0	761	0	2,000	10+	0	150—	0
23 —30.5	29.7	33.9	36.4	29.9	47.4	57.7	5.62	7.46	7.3	719	0	2,000	10	T	T	0
30.5—55	33.8	31.6	34.6	29.0	43.8	57.4	5.07	8.10	8.2	1,074	0	2,000	10	T	T	T
Ave. to W.D. 33 in.	26.6	40.1	33.3													
TEST AREA 35. Distichlis, Puccinellia, Agropyron.																
0 — 1.5	52.5	38.5	9.0	6.7	16.4	Would	2.65	6.77	5.0	354	T	400—	50	1,000	600+	0
1.5— 4	47.7	34.7	17.6	16.3	22.7	not	3.67	7.20	7.0	1,943	T	400—	50	2,000	600	0
4 — 8	29.2	39.8	31.0	27.9	37.1	take	4.53	8.60	8.9	13,500	2	1,000	100	6,000	600	0
8 —14	25.7	55.2	19.1	17.4	43.7	water.	4.80	8.50	9.9	13,900	T	1,000	100	5,000	600	T
14 —19	13.2	41.8	45.0	42.5	56.3	61.4	5.95	8.10	11.1	11,300	0	2,000	50	6,000	600	0
19 —37	14.3	29.2	56.5	50.2	66.8	63.1	5.55	7.70	7.5	11,200	0	1,000	50	5,000	300	0
37 —42	26.3	36.9	36.8	33.6	48.4	60.0	4.95	7.70	10.0	9,600	0	1,000	25	4,000	200	0
Ave. to W.D. 26 in.	24.4	40.3	35.3	31.9	47.7											
TEST AREA 36. Bouteloua, Stipa.																
1.5— 4.5	56.2	24.9	18.9	16.7	24.9	60.9	6.25	6.01	6.2	378	T	1,000	25	0	500	0
4.5—12	63.7	17.4	18.9	17.6	21.9	51.6	3.92	6.36	6.4	322	T	2,000	25	T	150	0
12 —19.5	68.0	12.3	19.7	18.8	22.2	47.2	3.40	6.28	7.1	386	0	2,000	50	T	150—	0
19.5—29	61.0	17.5	21.5	19.7	24.8	50.3	3.25	6.43	6.9	473	0	2,000	25	0	150—	0
29 —38.5	65.9	15.5	18.6	16.9	21.1	48.5	3.10	6.50	6.8	472	0	2,000	10+	0	T	0
38.5—41.5	67.1	14.2	18.7	16.9	21.1	47.4	2.80	7.70	7.8	440	0	3,000	10	0	T	0
41.5—51	62.1	18.3	19.6	17.7	22.5	50.8	3.75	8.00	9.6	465	T	2,000	25	0	T	T
51 —57	75.1	10.5	14.4	13.0	16.2	46.4	2.75	3.14	8.8	518	0	2,000	25	0	T	0
Ave. to W.D. 51 in.	63.7	16.7	19.6													

*Figures refer to approximate pounds per acre.

The frequency-abundance figures are useful in evaluating the relative importance of species in the type. The average and range in these figures for test areas 1, 2, 3, 4, 6, and 7, are for *Bouteloua gracilis* 96.5 (90.7-100), *Stipa comata* 68.6 (29.0-97.7), *Carex filifolia* 52.2 (0.2-100), *Carex stenophylla* (including some *C. pennsylvanica*) 35.3 (8.7-69.3), *Koeleria cristata* 16.3 (0-47.5), and *Agropyron smithii* 15.3 (0.3-66.3). All other species rated much lower, as for example, the more abundant characteristic forbs, *Malvastrum coccineum* 1.7 (0-5.7), *Chenopodium leptophyllum* 4.6 (0.8-15.9), *Lygodesmia juncea* 0.9 (0.1-2.6), *Plantago purshii* 3.7 (0-18.4),

Lepidium densiflorum 1.6 (0-4.4), *Hedeoma hispida* 1.4 (0-6.2), *Artemisia gnaphalodes* 5.2 (0-14.7), *Artemisia frigida* 7.1 (0.1-40.0), *Echinacea angustifolia* 0.9 (0-2.8), *Psoralea argophylla* 0.6 (0.1-2.1), *Gaura coccinea* 0.3 (0-0.9), and *Allium reticulatum* 1.5 (0-7.0). These figures indicate that the chief dominants are the first three grasses listed. Since the other three grasses have high frequency-abundance figures on some areas they should also rank as dominants but of less importance than the first three.

Except for *Bouteloua gracilis* considerable variation usually occurs in the frequency-abundance of each species on different areas in this type. The variation in *Stipa comata* appears to be partly due to replacement by other species as *Stipa spartea,* Calamovilfa, *Koeleria cristata,* and *Andropogon scoparius* in test area 7 where *Stipa comata* had a F x A figure of only 29.0. The brown soil extended to 38 inches in area 7 as compared to about 17 inches in area 1 and the moisture holding capacity was considerably higher in the surface layers in the former. Both of these conditions would be favorable to the more mesophytic species. *Carex filifolia* rated only 0.2 in area 7 and 100 in area 2. No explanation appears for this variation except that the greater abundance of taller species in area 7, due probably to more favorable moisture conditions, would handicap *Carex filifolia.* Variations in frequency and abundance of species within a type are due to a variety of causes as effect of competition between species, priority of invasion (the first dominant species to appear on an area, as *Carex filifolia,* may be difficult to replace), differences in soil conditions, and differences in treatment as grazing, mowing, or total protection.

The frequency-abundance figure for forbs (omitting *Draba nemorosa* and *Plantago purshii*) in this type averaged 37, ranging from 22 to 65 in 6 test areas. The high proportion of sand in area 6 is probably one of the causes for the low frequency and abundance of forbs in it as compared with most of the others. The high F x A number (65) of forbs in area 1 was due chiefly to *Chenopodium leptophyllum, Artemisia gnaphalodes,* and *Phlox hoodii.* The total number of species in this type was fairly high, averaging 44.7 and ranging from 33 to 53. The average number of species per quadrat averaged 14.6 (range 10.9-19.2). The variation in number of species on different areas within the same type is due to various causes such as successional age, degree of maturity of vegetation and soil, kinds of associated species and effects of resulting competition, former use of the area, and differences in soil or atmospheric factors, especially moisture. Area 3 had the lowest total number of species while area 7 had the highest number. Area 3 had much less sand in the soil, more carbonate, less potassium, shallower dark soil, and greater abundance of *Agropyron smithii* and *Carex filifolia.* It appears that area 7 presented more favorable soil conditions for a variety of species and a combination of dominant species (Bouteloua-*Carex*

stenophylla-Koeleria-Stipa-Calamovilfa) less exclusive in their domination than those on area 3 (Bouteloua-Agropyron-*Carex filifolia*-Stipa).

Characteristics of this type, as disclosed by the present study, may be summarized as follows:

1) Chief dominants: *Bouteloua gracilis, Stipa comata, Carex filifolia.* Less important dominants: *Carex stenophylla, Agropyron smithii, Koeleria cristata.*
2) Topography: Upland plateaus and gentle upland slopes, largely soil from residual material.
3) Moderately high total number of species in each example of the type (average 44.7, range 33 to 53), about three-fourths of these being forbs.
4) Soil texture usually sandy loam, averaging about 68 percent sand (53-87).
5) Fairly deep layer of dark soil ranging from about 17 to 33 inches thick.
6) Moisture-holding capacity of the soil was moderate ranging from 50 to 65 percent near the surface to 39 to about 58 percent in the deeper layers.
7) Loss-on-ignition was low ranging from 2 to 7 percent.
8) Effervescence with HCl began at various depths ranging from 13 to 60 inches below the surface.
9) The soil was usually slightly acid, pH 5.8 to 6.7, from the surface to average depth of 22.4 inches (5.5-38.5).
10) Carbonate contents were usually low to moderate, ranging from 2 to 15 percent.
11) Soil colloids variable, low to moderate, usually 12 to 30 percent.
12) Total soluble salts were low ranging from 281 to 680 p.p.m.
13) The soil was usually free from sodium (water soluble and exchangeable base) as tested by Morgan's Universal System.
14) Profile well developed.

2. *Western wheatgrass-grama-sedge type* (Fig. 4). Test areas 10, 11, 12, and 13 are classed in this type which usually occurs on fairly long, gradual clay slopes (see Fig. 4). Such slopes are common in the region. It appears that these slopes were formed by the deposition in valleys of material eroded from hills and buttes, represented now by remnants. Soil conditions are not stabilized because the slopes are subject to considerable runoff. Erosion proceeds rapidly when the vegetation cover is broken. Clay and silt may be deposited as the runoff from above is slowed up by the vegetation and more moderate slope. Since these slopes are subject to runoff, erosion, and deposition, development of both vegetation and soil is retarded. The density of the vegetation is often sparse, especially in drought years because these slopes tend to become deficient in soil moisture sooner than areas that are more level and contain more sand.

Frequency abundance averaged for *Bouteloua gracilis* 94 (75-100), *Agropyron smithii* 77 (55-100), *Carex filifolia* 81 (66-85) and *Stipa comata* 6 (0-16). Other grasses, as Koeleria, *Poa buckleyana,* and *Muhlenbergia cuspidata,* and one sedge, *Carex stenophylla,* were scarce. The F x A

index figure for forbs was low, ranging from 4 to 16 in the different test areas. The most common forbs were *Plantago purshii, Hedeoma hispida, Malvastrum coccineum, Linum rigidum, Chenopodium leptophyllum, Lepidium densiflorum, Phlox hoodii, Draba nemorosa, Gaura coccinea, Astragalus lotiflorus,* and *Lappula occidentalis.* The frequency-abundance index figures, as well as the percentages of cover secured by the point method, demonstrate that the dominants in the test areas studied in this type were *Bouteloua gracilis, Agropyron smithii,* and *Carex filifolia.* Observation of other areas showed that these three species were the chief dominants in this type.

Area 12 had a larger frequency-abundance of *Stipa comata* and *Koeleria cristata* and lower frequency-abundance of *Agropyron smithii* than the other areas in this type. These differences appear to be related to the greater amount of sand in the surface 10 inches in area 12 (ranging from 44 to 62 percent in area 12, but 20 to 38 percent in areas 10, 11, and 13); to the much lower amount of colloids (16 percent in area 12, but 28 to 33 in areas 10, 11, and 13; to the acid soil reaction (pH 6.6 to 6.8) in the surface 6 inches of area 12 but alkaline (pH 7.2 to 7.5) in the others; and to the smaller quantities of calcium and potassium in area 12.

Characteristics of the western wheatgrass-grama-sedge type are:

1) Dominants: *Bouteloua gracilis, Agropyron smithii, Carex filifolia.*
2) Topography: Fairly long, gradual slopes; valley-fill deposits.
3) Low total number of species ranging from about 20 to 29 in test areas, about three-fourths being forbs.
4) Soil texture usually clay loams, consisting of 30 percent or more of clay and less than 40 percent of sand.
5) Shallow layer of dark soil, 0 to 6 inches.
6) Moisture-holding capacity moderate, usually ranging from about 60 percent near the surface to 40 to 50 percent deeper.
7) Loss-on-ignition was usually moderate, averaging about 6 to 8 percent, but ranging from 2.6 to 17.7 percent.
8) Effervescence with HCl showed at the surface or began only 1 to 3 inches below.
9) The soil was usually alkaline throughout; pH 7.2-7.5 at the surface to 8.0-8.6 in the deeper horizons.
10) Carbonate contents ranged from moderate (7-8 percent) in surface layers to high in lower layers (15-31 percent).
11) Soil colloids high, usually 25 to 50 percent.
12) Total soluble salts were usually low (500-700 p.p.m.) to depths of 3.5-4 feet.
13) The sodium content was usually negligible but was high in the 27 to 45-inch layer in area 10. Calcium was usually medium high, potassium low.
14) Profile shows moderate development.

3. *Little bluestem type* (Figs. 1, 4). Test areas 25, 26, and 31 belong to this type. It occurs on slopes where snow drifts in and on northerly aspects of fairly steep slopes (10 to 20 degrees) of hills and plateaus. This type is widespread especially in the southern part of the Little Missouri Range

region. The soil material on these slopes appeared usually to be of residual origin, but in some cases was formed evidently by deposition.

Little bluestem is one of the first invaders on areas made bare by "step" erosion (see Fig. 4). Once established it is difficult for other grasses to displace it because of its dense and tall growth as long as soil moisture is adequate. Moisture conditions below the "step" are more favorable than on the general slope because snow tends to accumulate and runoff is retarded. As the "step" widens, unites with other steps, and becomes deeper as erosion extends up the slope the area of little bluestem may enlarge until it occupies most of a hillside. Little bluestem is also one of the first invaders in gulleys started by cattle trails and road ruts, and from these vantage places may spread with the course of erosion over a slope. Once established, the cover of little bluestem usually protects the slopes from excessive runoff and erosion. Since livestock ordinarily do not graze this grass the old leaves and stems accumulate on the surface. During drought periods, there is less growth and the livestock may become forced to graze it closely. The cover is thus reduced and runoff and erosion may become greatly accelerated. Grasshoppers aid in the denuding process because they also, are forced to feed on little bluestem during severe droughts.

The little bluestem type is of great ecological importance because it stabilizes areas subject to heavy runoff and erosion (see Fig. 1), holds drifting snow, hastens soil development because of the numerous roots to 3.5 feet in depth and large volume of herbage. In places little bluestem appears to be rather short-lived and to be succeeded on more moderate slopes by blue grama, western wheatgrass, needlegrass, and sedges.

The frequency-abundance analysis of the vegetation showed that *Andropogon scoparius*, with an F x A index figure of 100, was the chief dominant. In restricted places other grasses or sedges were important enough, perhaps, to rate as local dominants. The most abundant of these were *Bouteloua curtipendula, Koeleria cristata, Carex filifolia, C. stenophylla, C. pennsylvanica, Bouteloua gracilis,* and *Calamovilfa longifolia.* Characteristic forbs were *Echinacea angustifolia, Gaura coccinea, Helianthus rigidus, Senecio columbianus, Lygodesmia juncea, Calochortus nuttallii, Meriolix serrulata, Linum lewisii, Asclepias verticillata, Anemone cylindrica, Campanula rotundifolia, Heuchera hispida, Comandra pallida, Arabis holboellii, Drymocalis arguta,* and *Solidago* spp.

Characteristics of the little bluestem type are:

1) Dominant: *Andropogon scoparius.*
2) Topography: fairly steep slopes.
3) High total number of species per area, averaging about 50, of which about one-third are grasses.
4) The soil texture varied greatly in different horizons, ranging from sandy loam to silty clay. Most of the horizons were clay loam, silt loam, or loam.
5) The layer of dark soil was shallow, 1.5 to 7 inches.

6) Moisture-holding capacity of the soil was moderately high, 52 to 68 percent.
7) Loss-on-ignition was low, 2 to 8 percent.
8) Effervescence with HCl began on the surface.
9) Soil was usually alkaline throughout, pH 7.2 to 8.4.
10) Carbonate content was high, usually 20 to 30 percent.
11) Soil colloids high, 20 to 50 percent.
12) Total soluble salts moderately low, 312 to 743 p.p.m.
13) Calcium medium high to high, potassium and phosphorus low, sodium and chlorine negligible.
14) Profile not well developed.

4. *Sandgrass type* (Fig. 8). Test areas 21, 22, 23, and 24 have been classified in this type which is found widely on sandy ridges and hills in this region. The soil is apparently residual in origin. Both vegetation and soil are in moderately early stages of development. The high water absorbing capacity of the soil and the dense, tall growth of sandgrass prevent excessive runoff or erosion. Since Calamovilfa is no palatable to livestock and therefore usually not grazed it is not damaged in pastures. Plowing or excessive trampling may lead to wind erosion.

The average frequency-abundance of the most important grasses and sedges in this type shows *Calamovilfa longifolia* 59 (40-84), *Carex filifolia* 49 (16-84), *C. stenophylla* and *C. pennsylvanica* 58 (1-90), *Stipa comata* 35 (26-44), *Bouteloua gracilis* 29 (13-47), *Koeleria cristata* 17 (10-25), and *Andropogon scoparius* 9 (0-18). Although several of these species have high F x A index figures, Calamovilfa is the only one rated as a dominant because of its much greater height, deeply penetrating and numerous roots, and general vigor. This type is apparently developing into the first type, grama-needlegrass-sedge type. Calamovilfa is in control but factors are operating which are more favorable for growth of the secondary grasses than for Calamovilfa. Some of these factors are the shallow penetration of rainfall during the recent successive droughts, reduced height growth of Calamovilfa permitting more light to enter and the reactions of Calamovilfa roots upon soil development.

The F x A index figure for forbs was low in this type, averaging 12.5 (7-16). Some of the more common forbs were *Lygodesmia juncea, Psoralea argophylla, Aster multiflorus, Liatris punctata, Artemisia gnaphalodes, A. frigida, Asclepias verticillata, Phlox hoodii, Echinacea angustifolia, Chrysopsis villosa, Lithospermum linearifolium, Lesquerella arenosa,* and *Chenopodium leptophyllum.* This list resembles the one of forbs for the first type.

Characteristics of the sandgrass type are:

1) Dominant: *Calamovilfa longifolia.* Important secondary species; *Carex filifolia, C. stenophylla, C. pennsylvanica, Bouteloua gracilis, Stipa comata,* and *Koeleria cristata.*
2) Topography: Sandy ridges and hills, apparently residual in origin.

3) Moderately high total number of species (35 to 42), about two-thirds of which are forbs.
4) The soil texture is a highly uniform sandy loam, the sand content to depths of 5 and 6 feet averaging about 73 percent (60-87).
5) The depth to which the dark soil extended varied considerably, from 0 to 19 inches.
6) Moisture-holding capacity of the soil was moderately low, ranging from 41 to 53 percent.
7) Loss-on-ignition was very low, 2 to 4 percent.
8) The depth at which effervescence with HCl began varied greatly, from the surface in area 21 to below 72 inches in area 24.
9) Except in area 21 the soil showed acid reaction (pH 6.11-6.85) to depths varying from 39 to 69 inches. The rest of the soil varied from pH 7.04 to 7.70.
10) Carbonate contents were low in areas 22 and 23 (4.2 to 7.5 percent) but high in area 21 (15.2 to 16.1 percent).
11) Soil colloids were low, especially in area 21 (5.1 to 10.9 percent). The maximum amount was attained in area 23 with 23.4 percent.
12) Total soluble salts were low 252 to 588 p.p.m.
13) Calcium in the soil varied from low to high, potassium and phosphorus were usually low, sodium and chlorine showed only traces in some horizons.
14) Profile not well developed.

5. *Sagebrush type* (Fig. 7). In this type are included areas 18, 19, and 20. This type is widespread in the region occurring on flats along streams and in valleys. Best developed examples of the type were found usually on flats along the Little Missouri River and along creeks with permanent water as Garner Creek. This type is subject to flooding, erosion, and deposition due to storm waters which overflow the narrow stream channels. Stratification and heterogeneity are conspicuous in the profiles of this recently deposited, alluvial material.

The type is characterized chiefly by the gray-colored shrub, *Artemisia cana,* growing in dense or open stands. Most commonly it grows from 3 to 4 feet tall. Usually there is considerable grass growing in and between the bushes. While sagebrush, because of its abundance and height growth, is the major dominant, several grasses, *Agropyron smithii, Bouteloua gracilis,* and *Stipa viridula,* are of sufficient abundance and influence to rank as dominants but of less importance. The frequency-abundance of *Artemisia cana* averaged 48 (24-90), *Agropyron smithii* 88 (67-100), *Bouteloua gracilis* 41 (0-75), and *Stipa viridula* 34 (4-50). These index figures, which register only frequency and abundance, do not tell the complete story regarding dominance because the taller growth and greater volume of sagebrush are not incuded. Other species of grasses or sedges were very low in both frequency and abundance, appearing as accidental.

Forbs were usually not abundant in this type, the F x A index figure averaging 10 (5-19). The chief forbs, all with very low F x A indices, were: *Vicia sparsifolia, Lappula occidentalis, Musineon divaricatum, Malvastrum*

coccineum, Plantago purshii, Chenopodium leptophyllum, Linum rigidum, Lepidium densiflorum, and *Allium reticulatum.*

The absence of *Bouteloua gracilis,* the much lower frequency and abundance of *Stipa viridula,* and the higher frequency and abundance in area 19 as compared with areas 18 and 20 appear to be due to the greater amount of recent deposition of soil material in area 19. The stream channel is more shallow, the valley is narrower, and the laminations are much plainer in area 19. There were numerous other evidences of frequent flooding and deposition over area 19, as small gulleys, moist deposits, and débris in the branches of sagebrush. Bouteloua is not able, and Stipa has difficulty, to grow under these unstable conditions; but *Agropyron smithii,* with its extensive rhizomes, and Artemisia appear to thrive.

Characteristics of the sagebrush type are:

1) Chief dominant: *Artemisia cana.* Less important dominants: *Agropyron smithii, Bouteloua gracilis, Stipa viridula.*
2) Topography: Flats along streams and in valleys.
3) Total number of species was variable, 23 to 50, of which 75 to 80 percent are forbs.
4) Soil texture was variable in each horizon. Clay loam and clay were found more often than sandy loam, loam, or silt loam. The sand content reached as high as 78 percent in one horizon while in another horizon of the same profile the clay content was 58.6 percent.
5) The depth to which the dark soil had developed varied from none in area 19 to 10 and 11 inches in areas 18 and 20.
6) Water-holding capacity varied from low to high, 40 to 72 percent.
7) Loss-on-ignition varied from low to high, 2.4 to 13.4 percent.
8) Effervescence with HCl occurred in all horizons beginning at the surface.
9) Soil reaction was alkaline throughout, varying from pH 7.3 to 8.2.
10) Carbonate contents were moderately high ranging from 9.7 to 16 percent.
11) Soil colloidal content was variable, the weighted averages to the working depth ranged from 36 to 49 percent.
12) The amounts of total soluble salts were moderate, 537 to 1,220 p.p.m.
13) Calcium varied from low to high, potassium and phosphorus were usually low, in most horizons sodium was negligible but occasionally horizons with moderate amounts occurred, chlorine was negligible.
14) Profile usually not well developed.

6. *Saltgrass-western wheatgrass type* (Fig. 6). Areas 15 and 17 were classified in this type. These areas occurred on terraces 6 to 10 feet above intermittent or flowing streams. This type is subject to flooding, deposition, and erosion when the sod is broken. The stratified horizons show recent alluvial origin. Scattered young sagebrush, occurring in some areas, indicate that the course of succession may be into the sagebrush type, due possibly to improved drainage.

Agropyron smithii, F x A 46 and 100, and *Distichlis stricta,* F x A 46 and 88, were the chief dominants. *Bouteloua gracilis,* F x A 15 and 100,

was a less important dominant. *Stipa comata, Carex filifolia, Stipa viridula,* and a few other grasses were scarce.

Forbs were variable and low in F x A, 2 and 22, represented chiefly by ruderals as *Helianthus petiolaris, Iva xanthifolia, Plantago purshii,* and *Lepidium densiflorum.* Some additional species were characteristic but scarce as *Atriplex argentea, A. nuttallii, Chenopodium leptophyllum,* and *Musineon divaricatum.*

The greater frequency and abundance of Agropyron, Distichlis, and Bouteloua in area 17, as compared to area 15, were probably due to higher soil moisture throughout the season in 17. The creek bordering 17 (Fig. 6) has water in it throughout the year but in 15 the stream is usually dry.

Area 14 (Fig. 5) was similar to areas 15 and 17 but *Bouteloua gracilis* and *Stipa comata* were additional major dominants, making 4 in all. *Carex filifolia* and *Calamagrostis montanensis* were also present in 14 but not in 15 and 17. Frequency and abundance of forbs were greater also. This area was intermediate between types 1, 2, and 6. The terrace was higher above the stream than in areas 15 and 17. The soil profile was more fully developed, it was much less subject to flooding and the soil was more sandy.

Characteristics of the saltgrass-western wheatgrass type are:

1) Chief dominants: *Distichlis stricta, Agropyron smithii.* Less important dominant, *Bouteloua gracilis.*
2) Topography: Moderately low stream terraces subject to occasional flooding.
3) Total number of species was moderate, 28 to 36, three-fourths to four-fifths being forbs.
4) Soil texture was usually silt loam, varying from 26 to 40 percent sand in area 15, to 38 to 57 in area 17.
5) The layer of dark soil was shallow to moderate, 6 to 12 inches.
6) Water-holding capacity varied from moderate to high, 44 to 87 percent.
7) Loss-on-ignition varied from low to moderately high, 4 to 12 percent.
8) Effervescence with HC1 began at the surface.
9) Soil reaction was mildly alkaline, pH 7.2 to 8.3.
10) Carbonate contents were moderately high, 12 to 20 percent.
11) Soil colloid contents were moderately high, 20 to 30 percent.
12) The amounts of total soluble salts varied from moderately low to high, 603 to 7,200 p.p.m.
13) Calcium was medium to high, potassium trace to extra high, sodium varied from low to high below 20 inches, chlorine was negligible.
14) Profile poorly developed.

7. Saltgrass-alkali meadow grass type. Areas 16 and 35 (Fig. 11) are classified in this type which occurs on low stream terraces and other depressions in which drainage is poor. This type is subject to fairly frequent flooding, deposition, and erosion when the sod is broken. Stratification, indicating recent alluvial origin, was pronounced in area 16, but in area 35 columnar and prismatic structure occurred. The soil in area 35 is solonetz (Kellogg 1934).

The chief dominants were *Distichlis stricta* and *Puccinellia nuttalliana*. *Agropyron smithii* and *Hordeum jubatum* were abundant on some areas. Forbs were low in frequency and abundance. The most characteristic were *Dondia depressa, Grindelia squarrosa, Atriplex argentea, Plantago elongata, Chenopodium leptophyllum*, and *Lepidium densiflorum*, and *Opuntia fragilis* which was limited to area 35.

The greater abundance of *Agropyron smithii* and *Opuntia fragilis* on area 35 than on area 16 may be due to the greater age of the first area, thus giving more opportunity for these species to invade. The soil is usually saturated with water for a longer time each year in area 16 than in area 35.

Characteristics of saltgrass-alkali meadow grass type are:

1) Chief dominants: *Distichlis stricta, Puccinellia nuttalliana*. In some areas *Agropyron smithii* may be a lesser dominant.
2) Topography: Low stream terraces and depressions, drainage poor.
3) Total number of species was low, 24 in area 16, of which 19 were forbs.
4) Soil texture varied from loam to clay in the different horizons. Clay content in area 16 varied from 17 to 30 percent; in area 35, 9 to 56 percent.
5) The surface soil was grayish-brown.
6) Water-holding capacity was high, 55 to 63 percent. The soil samples from the upper 4 horizons, to 14 inches, in area 35 did not absorb water when the Hilgard pans were set in water for a long time.
7) Loss-on-ignition was low, 2.6 to 7 percent.
8) Effervescence with HCl began on the surface in area 16, at 4 inches deep in area 35.
9) Soil reaction was alkaline throughout except in the surface 1.5-inch layer in area 35 where it was mildly acid, pH 6.8. Most of the soil showed moderately high alkalinity, from pH 7.7 to 8.6.
10) Carbonate contents were moderately high in area 16 (18-21 percent), low in area 35 (5-11 percent).
11) Soil colloidal content was variable and usually high, 16 to 67 percent.
12) Soluble salt contents were usually very high, reaching 11,100 p.p.m. in the 4.5-15.5-inch layer in area 16 and 13,900 p.p.m. in the 8-14-inch layer in area 35. The top 1.5-inch layer in area 35 was low (354 p.p.m.).
13) Calcium was high in 16, low to medium in 35; phosphorus reached medium to high; potassium was extra high in the upper 19 inches of 35, but only traces in 16; sodium was medium in 16, extra high in 35; chlorine was negligible.
14) Profile poorly developed.

8. *Buffalograss type*. Only one area, 33, is included in this type. Buffalograss usually grows in small patches on the lower portions of some slopes, in small draws and depressions in some valleys, and on portions of scabby, gentle slopes or flats where the soil has a high clay content. In places it plays a part in the succession following solonization and solodization (Kellogg 1934); in other places its occurrence appears to be due to overgrazing, erosion, or other disturbances.

Characteristics of the buffalograss type are:

1) Dominant: *Buchloe dactyloides,* other species scarce.
2) Topography: See above.
3) Low total number of species.
4) Soil texture; usually clay, in area 33 most horizons had 37 percent or more clay.
5) Surface layer of dark soil 7 inches deep in area 33.
6) Water-holding capacity high, in area 33 usually 57 to 60 percent.
7) Loss-on-ignition moderately low, 3 to 6 percent.
8) Effervescence with HCl close to surface, at 7 inches in area 33.
9) Soil reaction mildly alkaline, pH 7.4-7.8.
10) Low carbonate content, 6.3-9.5 percent.
11) Soil colloids high, usually 45 to 62 percent in area 33.
12) Total soluble salts were usually high, mostly 1002 to 2456 p.p.m. in area 33.
13) Calcium low to medium high, potassium, phosphorus, sodium, and chlorine negligible to low.
14) Profile moderately well developed.

9. *Big bluestem type* (Fig. 4). Areas 27, 28, 29, and 32 were classified in this type. The small areas of this type were usually located on the lower parts of steep slopes, as in narrow valleys and draws. The type is important because it represents the best developed grassland in the region and it is unexcelled for summer grazing. This type, evidently, requires more moisture than that furnished only by direct precipitation. The additional moisture is received by runoff from slopes above and possibly from melting snow drifts and seepage. Vegetation and soil showed maximum development in this region, more typical of the true prairie in eastern North Dakota. The small areas of this type in this region, then, are minute outliers of the true prairie.

The F x A index figure of *Andropogon furcatus,* the dominant, ranged from 95 to 100. Other important grasses were *Andropogon scoparius* (33-95), *Koeleria cristata* (1-12), *Bouteloua curtipendula* (1-22), *Carex stenophylla* (0-53), and *C. pennsylvanica* (0-51).

The frequency and abundance of forbs were high, F x A ranging from 24 to 41 percent. The most numerous were *Astragalus hypoglottis, Helianthus rigidus, Echinacea angustifolia, Campanula rotundifolia, Cerastium arvense, Anemone cylindrica,* and *Psoralea argophylla. Rosa suffulta* and *Symphoricarpos occidentalis* occurred frequently due to more favorable soil moisture conditions. Area 28 had a greater number of species, greater frequency-abundance of forbs and of more mesophytic grasses as *Stipa spartea* and *Elymus glaucus* and less *Andropogon scoparius* and *Bouteloua curtipendula* than areas 27, 29, and 32.

Area 30 (Fig. 9) may be considered as an example of the highest mesophytic development of the big bluestem type, found only where soil moisture is especially suitable. *Sporobolus heterolepsis* was dominant with *Andropogon furcatus.* Other prairie species in greater abundance or restricted to this area were *Panicum virgatum, Elymus glaucus, Stipa spartea, Agropyron tenerum, Juncus balticus, Carex pennsylvanica, Avena hookeri,*

Lilium umbellatum, Helianthus subrhomboideus, H. maximilliana, Liatris scariosa, and *Glycyrrhiza lepidota.* There was a total of 86 species in this area, averaging 20.3 species per m^2 quadrat.

Characteristics of the big bluestem type are:

1) Dominant: *Andropogon furcatus.* On dry portions *A. scoparius* is a less important dominant, on moist areas *Sporobolus heterolepis* is also dominant.
2) Topography: Lower parts of slopes where moisture in addition to direct precipitation is received.
3) High total number of species, 41 to 63, three-fourths to four-fifths being forbs.
4) Soil texture, loam to sandy loam, usually 40 to 55 percent sand.
5) Layer of dark soil usually deep. In area 28, however, it was only 9 inches deep, in the others 15 to 46 inches.
6) Water-holding capacity was high, especially in the surface 4 to 6-inch layer where it was usually 90 percent or more. Below this it varied from about 50 to 75 percent.
7) Loss-on-ignition was high in the surface 4 to 6 inches, 10 to 13 percent; low to moderate below, 4 to 9 percent.
8) The depth at which effervescence with HC1 began, varied from 4 to 25 inches, 33 inches in area 30.
9) Soil reaction was usually acid to depths of 20 to 32 inches. In area 28, the pH was as low as 5.5 in the surface 4 inches.
10) Carbonate contents varied considerably, from 5 to 27 percent.
11) Soil colloids varied from low to high, but usually ranged from 18 to 35 percent. They were noticeably lower in area 30, 8 to 17 percent.
12) Total soluble salts were low, 329 to 678 p.p.m.
13) Calcium content was usually medium, potassium was usually low, but in area 30 it was extra high to depth of 18 inches.
14) Profile well developed.

Miscellaneous areas. Numbers 5, 8, and 9, located on gradually sloping higher stream terraces were intermediate between types 1 and 2. The dominants on these areas were *Bouteloua gracilis, Agropyron smithii, Stipa comata,* and *Carex* spp. *Koeleria cristata* also occurred on each of these areas. The representation of forbs was similar to types 1 and 2. The total number of species varied from 18 to 42. Soil characteristics were usually intermediate between the two types as soil texture which was clay loam, depth of dark soil 7 to 10 inches, effervescence began at 7 to 10 inches and surface soil mildly acid or alkaline. It appears that soil and vegetation on these areas were transitional in development from the western wheatgrass-grama-sedge type to the grama-needlegrass type.

Area 34 (see Fig. 10) was the only locality found that showed dominance of *Bouteloua gracilis* and *Poa buckleyana.* Other species were *Malvastrum coccineum, Plantago purshii, Artemisia dracunculoides, Agropyron smithii, Stipa viridula, S. comata* and a few additional forbs. The soil contained an unusually high percentage of clay and silt averaging 73 to the

working depth, and the hard columnar structure indicated that this may have been a solonetz soil.[1]

DISCUSSION

Classification of vegetation in western North Dakota is difficult because of the great heterogeneity due to variations in topography, soil conditions, wind and water erosion, water penetration, and to the various kinds of succession and stages in succession (see Figs. 1, 5). Seres are occurring on recently eroded banks, on recent depositions, on saline depressions, on sandy hills and ridges, on abandoned cultivated lands, and on areas depleted by grasshoppers, drought, and overgrazing. Since successional sequences have not yet been determined it is not possibe to make a classification which will show relationship between the different types. The importance of succession in the tall-grass prairie has been discussed by Weaver and Fitzpatrick (1934, pp. 281-288).

In the Little Missouri country it appears that the grama-needlegrass-sedge type (Figs. 2, 3) on upland plateaus and gentle upland slopes is nearer stabilization with climatic conditions than any of the other types studied. This type has had the longest period of time in which to reach stabilization. The western wheatgrass-grama-sedge type (Fig. 4) appears to be a successional stage on slopes developing in the direction of the first type. Areas 5, 8, and 9 appear to be further along in this succession than the western wheatgrass-grama-sedge areas. The big bluestem type is a more mesophytic type than the grama-needlegrass-sedge type but it cannot be considered climatically stabilized because it is located in places where moisture in excess of direct precipitation is received (Fig. 4). It does not seem possible that direct precipitation in this region can support this true prairie type (Fig. 11). The little bluestem type appears to be a successional stage following erosion on many slopes (Fig. 4). The sandgrass type is a successional stage on sandy areas (Fig. 8). The sagebrush type (Fig. 7) appears to be a successional stage on terraces where soil moisture is usually available in the subsoil throughout the season. As the stream erodes a deeper channel, and the terrace becomes drier, types 2 or 1 may replace the sagebrush type. The saltgrass-western wheatgrass and the saltgrass-alkali meadow grass types belong in a halosere on poorly drained or solonetz soils (Fig. 11). Buffalograss communities occur in secondary seres following cultivation, overgrazing, and salinization. The course of plant succession in relation to soil characteristics and development requires long-continued investigations on areas reserved for this purpose. (Tansley 1935; Shelford and Hanson 1936).

Other types, not treated in this paper, occur in the region, as the shrub types in valleys (Symphoricarpos, Rosa, Ribes, Prunus), the *Pinus ponderosa* type near Ranger, the Juniperus type, the Fraxinus-Acer type in

[1] Because of the acid reaction in the leached portion of the profile above the columns, Dr. Charles E. Kellogg, Chief, Division Soil Survey, U. S. Bureau of Chemistry and Soils, suggests that it would be more accurate to say "solodized solonetz" rather than "solonetz." (See profile description).

draws, and the *Populus deltoides* type on the Little Missouri River floodplain (see Figs. 1, 5). The early successional stages following erosion, deposition, and cultivation, have not been discussed, but all the major grassland types are included.

The problem of the relation of vegetation and the soil is one of exceeding complexity. The soil and the vegetation are both dynamic unities developed and controlled largely by the environmental forces acting upon them. Soil science has stressed the importance of native vegetation in the development of the soil. Ecological studies have shown the important influence of the soil on the development and structure of native vegetation.

Observation has shown that some plants grow better on certain soils than on others, and that certain native plants indicate soils suitable for raising some kinds of crops while other native plants indicate that the soil is unsuitable for the same crops. Considerable study has been devoted to the relation of forest cover to soil conditions but the relation of grassland to soil has not been investigated to nearly as great an extent.

Clements (1920) has summarized the earlier work on the relation of vegetation type to soil type. Kearney, Briggs, Shantz, McLane, and Piemeisel (1914) studied the vegetation of the Tooele Valley, Utah, with the object of determining and correlating the distribution of the vegetation with the physical and chemical properties of the soil. They found relationships between moisture content, soil texture, alkali salts, and vegetation.

Aldous and Shantz (1924) distinguished over 100 vegetation types in the arid and semiarid portions of the United States and evaluated them as to grazing and agricultural use. Shantz and Piemeisel (1924) distinguished vegetation types characteristic of certain soil conditions in the southwestern desert region, emphasizing particularly salt content and water relations. Newton and Nowosad (1933) in Quebec studied the relation of three types of soil to the flora of open and woodland permanent pastures. Cole and Dubey (1932) described the value of permanent pastures in Romney Marsh, England, in relation to soil profile, emphasizing soil texture and drainage conditions.

Frolick and Keim (1933) found the influence of the ground water table and soil texture to be the chief factors in determining the existence of distinctive plant communities in the prairie hay district of Nebraska. Steiger (1930), also in Nebraska, found the water content of the soil the most important factor determining differences in the structure of the vegetation.

The vegetation types are principally distinguished on the basis of the dominant species in the plant association and the topographical situation (see Figs. 1, 4, 5). This linkage between topographical position and the nature of the vegetation cover is best explained on the basis that different topographical situations present different environments for the development of the vegetation and soil types. This has long been recognized by soil sur-

veyors who frequently correlate differences of soil characteristics and, hence, soil series, with situation of the soil. The topographical position of a type is often an indicator of the geologic material from which the soil has been developed and of soil moisture conditions.

A comparison of the data for the test areas of the different types shows that there is considerable difference in textural composition between the profiles of the areas within the different types, as well as between types (see Table 1). Yet in general there is a similarity in textural composition of areas within types, while there is considerable variation between types.

Textural heterogeneity between types is indicated by changes in the structure of the vegetation. The working depths of the roots in the various vegetation types furnish a fairly good index to textural differences since they represent, except where influenced by other conditions, the depth of moisture penetration. Thus in the first two types moisture penetration is about 30 inches. This is further confirmed by the tendency of these types to accumulate carbonates in a definite horizon at this approximate depth. In the sandgrass type, on the other hand, the percentage of total sands is greater and the texture is somewhat coarser, for the working depth indicates that moisture penetrates on the average about twice as far as in the first type.

Textural differences also show their influence in another way. One of the outstanding differences between the grama-needlegrass-sedge and the western wheatgrass-grama-sedge types is in the total number of species found on each of the two types. Another difference is the much larger percentage of finer materials in the soil of the second type. The fact that a lower total number of species seems related to the higher percentage of finer material in the profile indicates the influence of texture on producing heterogeneity in vegetation. It seems likely that the effect here is an indirect one and is related to the wilting coefficient.

However, soil texture seems intimately bound up with that of soil moisture in influencing the composition of the vegetation (Frolick and Keim 1933, Steiger 1930). Metzger (1935) found that a low moisture supply tends to show soil heterogeneity, as measured by crop yields, while a high moisture supply seems to obscure it. Thorp (1931) related soil profile and precipitation to the vegetation in Wyoming.

Within a region where the precipitation is essentially the same and other climatic factors are largely similar, an increased supply of moisture in the soil will be indicated by a difference in vegetation. In general there are two sources of additional moisture, the presence of a water table, or seepage from other areas. Five of the different grassland vegetation types are produced under conditions where additional soil moisture is available. They are little bluestem, big bluestem, sagebrush, saltgrass-western wheatgrass, and saltgrass-alkali meadow grass (Figs. 4, 5, 6).

The little bluestem type and the big bluestem type apparently receive moisture by seepage from surrounding areas (Fig. 4). Their location on slopes suggests that moisture that is received on other areas by means of precipitation percolates through the soil and, meeting impervious layers, seeps out to become available to the roots of the bluestems. The profiles of these types were more moist than the profiles of grama-needlegrass-sedge, western wheatgrass-grama-sedge and sandgrass types. The moisture supply seems to be particularly favorable where the big bluestem type is developed. The flora of this type compares favorably with that of the true prairie developed under an annual rainfall of over 20 inches.

The sagebrush type and the saltgrass types (Figs. 5, 6) are developed under the influence of a water table that is within the range of the roots at least for a part of the season. The water table is generally deeper under the sagebrush type than it is under the saltgrass types. In the latter the presence of a water table close to the surface may be a limiting factor in root growth. This is indicated by the relatively shallow working depth of the roots. The high content of alkali salts is also an important factor influencing the development of the vegetation and soil of the saltgrass types (Table 1).

Kelley (1922, 1923) found that soil acidity influences the flora to a considerable extent, although he concludes that it is possibly never the single controlling factor in plant growth. Geisler (1926) found nothing to indicate that soil reactions are responsible for species distribution in the Cincinnati region. Young (1934) found a certain relationship between soil reaction and plant distribution, particularly in regard to the high acidity of certain soil types.

The soil reactions of most of the types studied in this investigation were alkaline. Only in the grama-needlegrass-sedge, sandgrass and big bluestem types was there significant acidity, and in these types the general range of reaction of the surface horizons was usually mildly acid. While this may have some bearing on the nature of the vegetation, the effect seems slight in comparison with the influence of the factors of moisture, soil texture, and soluble salts.

In the grama-needlegrass-sedge type the acidity of the surface horizons seems to indicate the relative age and maturity of this type as compared with the others. To quote Marbut (1928, p. 192): "It seems to be possible for the solution to become acid in that part of the zone where the amount of moisture available is still too small to prevent the zone of carbonate accumulation in part of the solum, but is large enough to finally remove the bases from the upper part of the solum and produce an acid soil. . . . but if the local environment were to remain unchanged through earth crustal movements, or by any other processes, long enough, it is apparent that the surface may possibly become acid." The acidity of the surface of some areas of the sandgrass type and the big bluestem type is suggestive of leaching, in the first case

influenced by the coarser texture of the material and in the second case by the excess moisture supply.

In addition to the factors examined in this study there are many others that should be investigated. Kellogg (1930) has emphasized the importance of base exchange in relation to plant growth. Jenny (1935) has correlated the units of base exchange material present in the soil with the growth of bluegrass in Missouri grasslands. The relation of organic matter and nitrogen content to soil texture is important, as has been pointed out by Russel and McRuer (1927). Definite soil moisture readings taken at different times during the season in the different types would be of great value.

SUMMARY

1. Characteristics of 36 areas of grassland in the Little Missouri region of western North Dakota were studied, chiefly during the summer of 1935. These 36 areas were classified in 9 vegetation types.

2. The 9 major types were 1) grama-needlegrass-sedge, 2) western wheatgrass-grama-sedge, 3) little bluestem, 4) sandgrass, 5) sagebrush, 6) saltgrass-western wheatgrass, 7) saltgrass-alkali meadow grass, 8) buffalograss, 9) big bluestem.

3. Botanical analyses of the vegetation were made by the frequency-abundance and point methods. Soil profiles were described in the field and soil samples from the various horizons were analyzed in the laboratory for chemical and physical characteristics. The characteristics of each type are summarized under "Classification of Test Areas into Types."

4. The 9 types differed chiefly in botanical composition, topographic location, thickness of surface layer of dark soil, depth at which effervescence with HCl began, acidity or alkalinity of the surface horizons, total concentration of soluble salts, sodium and carbonate contents, soil texture, and colloidal content.

5. The results show a definite relationship between soil heterogeneity and vegetation heterogeneity. There are distinctive soil differences and vegetation differences between the types. The mechanical analyses of the soils indicate heterogeneity in textural types which corresponds, in a measure, to the heterogeneity in grassland vegetation types but it is not assumed that textural differences are chiefly responsible for vegetational differences. Topographical position is important because different topographical situations present different environments for the development of vegetation and soil types. Although the exact role of each influencing factor has not been determined the duration of available soil moisture, depth to the water table, concentration of salts, and stage in various successional seres, are all important in determining vegetation types in this region.

6. The grama-needlegrass-sedge type appeared to have reached the highest degree of stabilization in relation to the climate, and the soil of this type

most nearly approaches the typical profile of the dark brown soils. The big bluestem type appeared to depend upon moisture additional to that received by precipitation. The other types appeared to be successional stages following erosion, deposition, salinization, overgrazing, or cultivation.

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THE EFFECT OF VEGETATION ON THE GROWTH OF LONGLEAF PINE SEEDLINGS

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[1] Former field assistants Lincoln Ellison and Allan G. Watkins rendered valuable assistance in the installation of the plots and in some of the subsequent field work.

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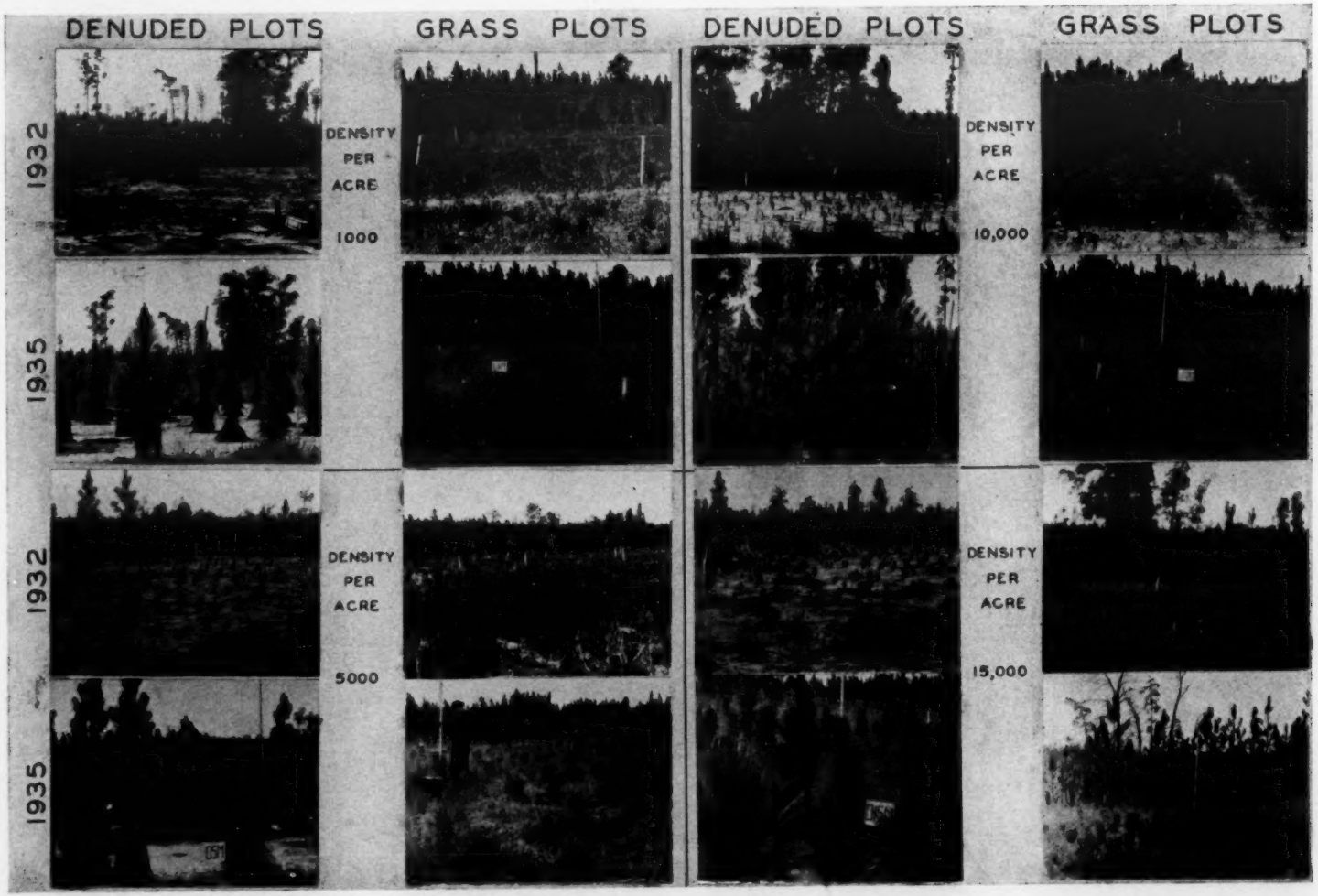
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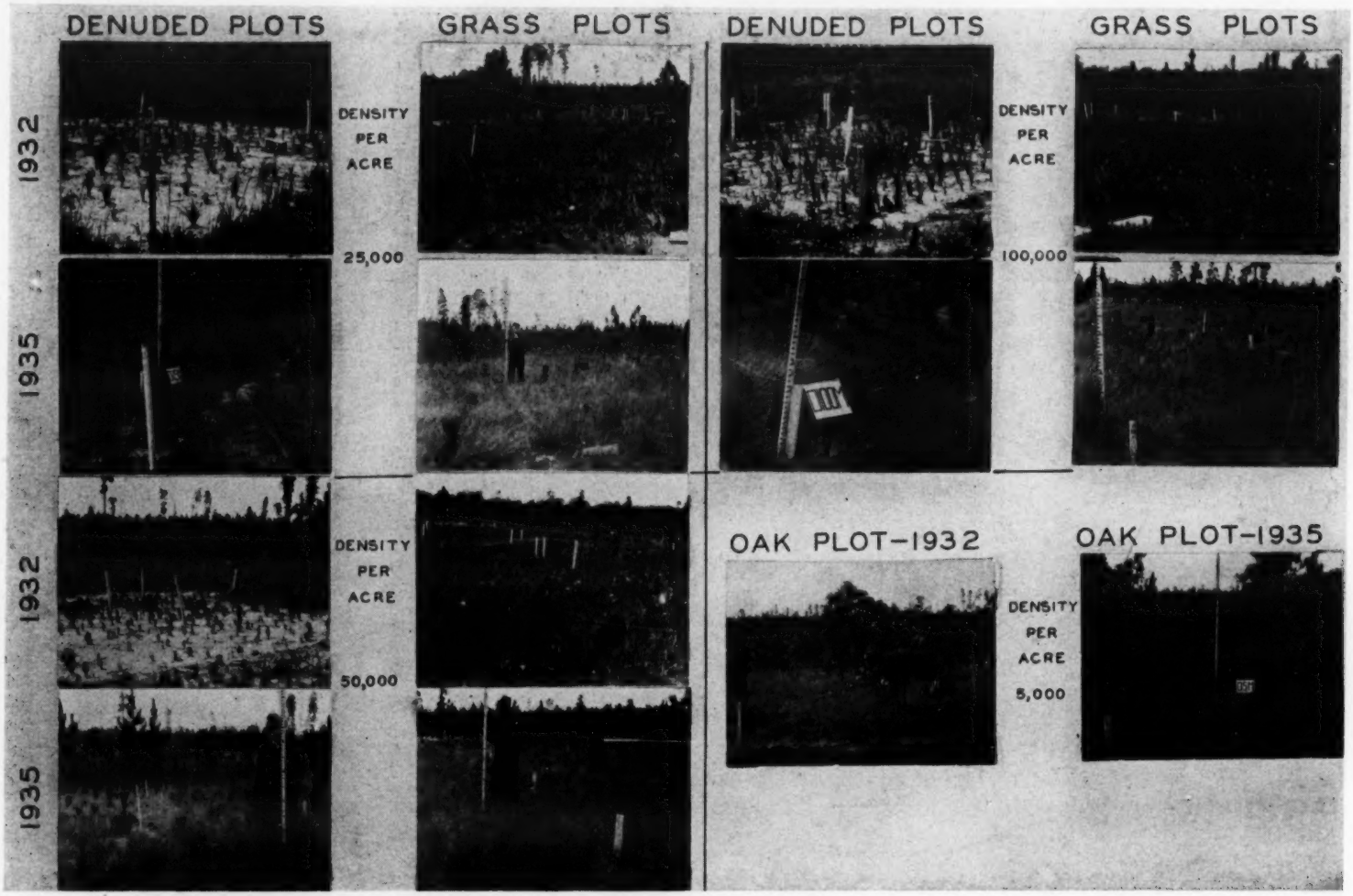
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THE EFFECT OF VEGETATION ON THE GROWTH OF LONGLEAF PINE SEEDLINGS

INTRODUCTION

Seedlings of longleaf pine (*Pinus palustris* Miller) growing under natural conditions exhibit characteristics which are not found among the other species of southern pines. The seeds of this pine germinate in autumn and by spring the seedlings generally have already shed their cotyledons. Also unlike the seedlings of other pines, those of longleaf pine develop a carrot-like taproot during early life and seem to endure a variety of site conditions. The greatest difference between longleaf pine seedlings and those of the other pines, however, is in the slow growth of the stem during the first few years. Even 4 or 5 years (and often longer) after germination the stem is hardly visible above ground, and the long leaves are often indistinguishable from the surrounding grasses (Fig. 1).

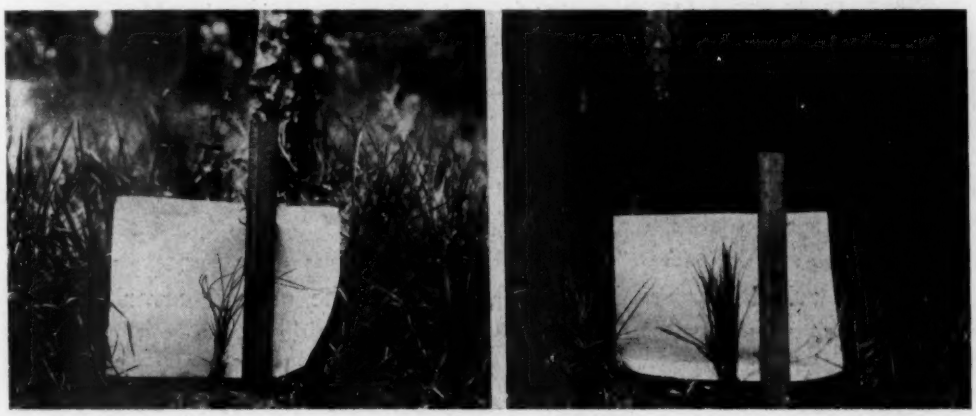

FIG. 1. Typical longleaf pine seedlings growing under natural conditions. At the right is a 7-year-old and at the left a 4-year-old seedling.

Not only do longleaf pine seedlings differ from other pine seedlings in the rate of growth of their stems, but they also differ among themselves. It is not uncommon to find longleaf pine seedlings 8 years old having a stem height of but 3 centimeters (1.18 inches), while other seedlings of the same species only half that age may be four times as tall. Various explanations have been offered for such differences in growth. The site is frequently regarded as the cause of the growth differences. Sometimes annual fires are blamed for the retardation in growth of the seedlings. Recently Siggers (1932) has shown that the brown-spot leaf blight (*Septoria acicola* (Thüm.) Sacc.) definitely retards the growth of longleaf pine seedlings through causing premature defoliation. Obviously all these factors may operate in nature,

either singly or in combinations, and the degree of the effect on the growth of the pines depends on the intensity of the factors.

Root competition is another factor that has sometimes been mentioned as the cause of the slow growth of longleaf pine seedlings, but the effect of this factor has been observed mostly in the field. It was the object of this study to determine definitely whether the vegetation commonly associated with pine seedlings affects their growth. Inasmuch as the vegetation is composed of grasses, herbs, scrub oaks, and pine seedlings, the study was divided into three parts: (1) the effect of the ground cover (grasses and herbs) on the growth of pine seedlings; (2) the effect of the number of seedlings occupying a definite area (density of stocking) on the rate of growth of their stems; and (3) the effect of the ground cover together with scrub oaks on the rate of growth of the pine seedlings growing in that area.

RESUMÉ OF LITERATURE ON COMPETITION

Competition among plants was first suggested by Petrus de Crescentiis as early as 1305. Later, Buffon (1745), Duhamel du Monceau (1760), Varenne de Fenille (1790), De Candolle (1820), Darwin (1859), and Nageli (1874) all made reference to the same subject. In 1904 Fricke challenged the commonly accepted idea of his day that competition among plants was mainly for light, and stated that competition for moisture among the roots of plants was even more important. He arrived at this conclusion by surrounding a stand of *Pinus silvestris* Linn. with a trench, severing the roots of adjacent plants, and freeing the plants in the enclosed area from competing roots. He found that in this area the young suppressed trees showed a marked increase in growth, and that the ground cover changed to a luxuriant stand, including species not found outside of the trenched area. He also sowed seed of pine, spruce, and oak in areas, which he surrounded with a trench. Here again not only was there an increase in growth of the seedlings, but also the germination was much better than in areas that had not been trenched. The moisture content of the soil in the trenched area was two to three times as great as in the untrenched areas.

Clements in the same year (1904) pointed out that competition was keener between species of like form than between those of dissimilar form and that the degree of competition increased as the density of the stand increased. Working with seedlings of *Pinus contorta* Loudon, Clements (1910) found that competition among the pine seedlings for water was very keen whenever their roots entered the same area, and particularly when the water content was relatively low. Competition for light, however, did not begin until height growth of the seedlings was well under way.

According to Sherff (1912), two or more species may live together without competing with each other if their roots lie at different depths, or

even if the roots lie in the same depths, if their demands on the soil are unlike. This was later confirmed by Salisbury (1924).

Aaltonen (1923) regarded light as a subordinate factor in the forest and emphasized the fact that the struggle for room is influenced by the subterranean rather than by the aerial parts of a tree. In a later paper (1926), he considered the lack of seedlings near old trees as due to competition for water and mineral foods and he reiterated his earlier statement that the space arrangement of the aerial parts of trees was decided by their roots and the competition existing between them in the ground, thus substantiating the views of earlier workers, Cotta, Borggreve, and Fricke. Aaltonen held the competition among even-aged trees to be even more important than that between seedlings and the mother tree.

Pearson (1923) found that bunch grasses in the Southwest retard the development of *Pinus ponderosa* Lawson seedlings. He attributed this retardation mainly to root competition. Yapp (1925) regarded competition as the chief factor in the establishment of a plant community, and Burns (1927) found that leaf development was influenced principally by the water content of the substratum and that the amount of water in the soil affected the density of the crown more so than did the light.

Fabricius (1927) laid out a trenched and an untrenched plot under a mature, well-closed spruce stand and found that on the trenched plot the seedlings were dark green and apparently more vigorous than those on the untrenched plot. On the trenched plot the annual growth in height of the seedlings was nearly six times that of the seedlings on the check plot. In a later paper (1930), he showed that a deficiency of water and a deficiency of light produced by the old stand each caused a distinct retarding of the growth of the seedlings under the canopy, and he concluded that root competition played a very important rôle in the growth of seedlings in a stand of older trees. In fact, where light was sufficient, root competition acted as the limiting factor.

According to Clements, Weaver, and Hanson (1929), competition among plants begins when the immediate supply of a single necessary factor falls below the combined demands of the plants. Competition, they claim, is a combined need in excess of the supply. It exists only where two or more individuals together seek more than is afforded by the space they occupy. Plants, they state, compete mainly for light, water, and nutrients, water being most important and nutrients least.

Toumey and Kienholz (1929) found that during the driest part of the year there was two to nine times as much moisture in the upper 6 inches of the soil in a plot surrounded by a trench as in that of an untrenched plot. They attributed this difference wholly to the elimination of root competition in the trenched plot. When the soil moisture was abundant, trenching exerted little influence on the amount of available moisture present in the

soil. They also found that on the untrenched plot the vegetation, eight years after the establishment of the plots, remained very sparse, while the trenched plot was covered by a dense mass of vegetation; on the untrenched plot, the density of the vegetation was 8.1 percent, while on the trenched plot it was 80 percent. The hemlocks on the untrenched plots averaged 2.5 inches in height, while on the trenched plot they averaged 37.7 inches. The differences were attributed to the lack of root competition on the trenched plot, resulting in a higher moisture content of the soil. These results substantiate those obtained previously by Phillips (1928). Pearson (1930), however, claims that even though trenching may increase moisture content, an increased soil temperature is likewise necessary for ponderosa pine in Arizona.

Coster (1933) found that when a teak plantation adjoins an older crop, the trees at the edge are behind in development and some even die. Experimentation proved that this was caused by the competition of the older roots and that competition for nutrients is negligible. Coster also found that when teak is mixed with other species, the diameter increment is markedly affected. He recommends that ditches be dug around younger plantations and even in blanks where replacements are made. Mixed plantings for teak are undesirable because of the unfavorable effect of root competition on the growth of teak. He concludes that on infertile soils thick undergrowth on areas protected from fire hinders the growth of teak.

HISTORY AND DESCRIPTION OF THE EXPERIMENTAL AREA

The experimental area is located between parallels 30° 48′ and 30° 50′ North Latitude in Washington Parish, 10 miles northwest of Bogalusa, Louisiana.

The area was formerly occupied by a stand of old longleaf pine, the dominant trees of which reached a height of over 110 feet. In 1920 the area was burned over prior to seedfall and the trees were cut. The logging took place in October and November, during an unusually heavy seedfall. Because many of the tree tops were left on the ground immediately after logging, the seed, which under normal conditions would have been widely scattered, remained on the ground in dense patches. This condition resulted in a very dense stand of seedlings. When examined in 1932, 12 years after seedfall, the number of seedlings still ran from 30 to 435 to the milacre[1] and most of them were still in the "grass stage"—that is, their crowns were below or on the same level with the surrounding grass tops, making the seedlings often indistinguishable from the grass. The area itself at the time of the establishment of the experiment was sprinkled generously with scrub oaks, principally *Quercus marilandica* Muench. and *Q. stellata* Wang. Saplings of longleaf pine, presumably of the same age (12 years old) as the seedlings and more than 6 feet in height, were scattered over the area. Work was

[1] An area 6.6 feet square comprising 0.001 acre.

started on the establishment of plots on March 23, 1932. By August of that year all the plots were established and data on various environmental factors were being collected.

The area is gently rolling and about 53.3 meters (175 feet) above sea level. Washington Parish lies in the geologic formation known as the Citronelle of the Gulf Coastal Plain (Matson and Berry 1916). The original surface of this formation sloped gently towards the Gulf, but at present the surface consists of slopes interrupted by terraces. In a few places remnants of the original surface of this formation may be seen, but these are frequently covered with water. The materials of the lower plain of the Citronelle formation were laid down toward the end of the Pliocene. The soil on the experimental area is predominantly Ruston fine sandy loam, but in places there are also outcroppings of Orangeburg fine sandy loam. The entire experimental area is well drained.

The vegetation on the area was typical of the upland soils of the longleaf pine belt (Pessin 1933). Three strip transects running east to west were laid out and the vegetation on these listed in April and again in August. These strips were 40.2 m. apart and each was 20.1 m. long and 19.0 cm. wide. Following are listed the plants found on the area together with the relative proportion of the ground cover occupied by each species. The pines and the oaks are omitted from this list, since these are considered separately.

VEGETATION ON THE EXPERIMENTAL AREA

Species	*Percent of population*
Panicum aciculare Desv.	18
Andropogon scoparius Michx.	17
Andropogon elliottii Chapm.	16
Lasiococcus dumosus Small *(Gaylussacia dumosa)*	14
Helianthus radula T & G.	10
Andropogon tener Kunth.	5
Drosera brevifolia Pursh.	3
Cerothamnus ceriferus Small *(Myrica cerifera)*	3
Panicum strigosum Muhl.	3
Pityopsis graminifolia Nutt. *(Chrysopsis graminifolia)*	3
Gracca virginiana L.	2
Crotalaria purshii D. C.	2
Cyanococcus myrsinites Small *(Vaccinium myrsinites)*	1
Tithymalopsis corollata Small *(Euphorbia corollata)*	Scattered
Pinguicula lutea Walt.	"
Pilostaxis lutea Small *(Polygala lutea)*	"
Stylosanthes biflora B. S. P.	"
Viola sp.	"
Trilisa odoratissima Cass.	"
Rhynchosia simplicifolia Wood	"
Gnaphalium purpureum L.	"
Laciniaria graminifolia Kuntze	"
Elephantopus tomentosus L.	"

Hypoxis hirsuta Coville	Scattered
Smilax bona-nox L.	"
Rhus copallinum L.	"
Phlox pilosa L.	"
Sisyrinchium graminoides Bicknell	"
Pteridium aqualina Kuhn.	"

The last 16 species compose about three percent of the plant population.

CLIMATE

Data collected in Franklinton, Louisiana, 11 miles west of the plots, showed that for six years (1926-32) the mean annual rainfall for this region was 61.31 inches. The mean temperature during the winter months for this period was 58.5°F.; during the spring months 64.3°F.; during the summer months 79.3°F.; and during the autumn 66.9°F. The mean annual temperature for the period between 1926 and 1932 was 67.2°F. The average date of the last killing frost was March 6 and the average date of the first killing frost was November 8. For each year there were approximately 246 frost-free days.

When the area was selected for this study a weather shelter was erected in which a Friez hygrothermograph was installed to record the relative humidity and the temperature of the atmosphere. The instrument was placed at 0.6 m. above ground. The velocity of the wind at the same height was measured by means of a 3-cup Friez anemometer, and the evaporation rate was determined by means of standardized Livingston spherical white porus clay cup atmometers equipped with mercury rain-correcting valves. The reservoir supply bottles were of 1-liter capacity. All the readings were corrected by the coefficients to the standard. At frequent intervals the cups were cleaned with alcohol to remove the algal growth which sometimes accumulated at the base of the sphere. Due to the prevalent high temperature, the necks of the cups had to be reshellacked at intervals of about six weeks. The amount of water evaporated was measured weekly and calculated on the basis of average daily evaporation. The rainfall data were measured with a standard Weather Bureau type rain gauge and the amount was recorded daily.

The temperature, relative humidity, and wind data for the experimental area for the growing seasons (April to October) of 1932, 1933, and 1934 are summarized in Table 1.

TEMPERATURE

The data indicate that the mean temperature during the growing season differed very little from year to year. In 1932 the mean temperature for the growing season was 73°F.; in 1933, 74°F.; and in 1934, 75°F. The average daily maximum temperature of 90°F. and above in 1932 occurred in July and August; in 1933 in June, August, and September; and in 1934 in June, July, and August.

WIND

The windiest months recorded during 1932 were May and September; in 1933, April, May, and July; while in 1934, May alone showed an average wind velocity of over two miles per hour.

RELATIVE HUMIDITY

In 1932 and 1934 the average daily relative humidity was lowest in April and in 1933 it was lower in June than in April.

TABLE 1. AIR TEMPERATURE, RELATIVE HUMIDITY, AND WIND VELOCITY ON THE EXPERIMENTAL AREA

Month	Mean Temperature (F.)			Temperature (F.)						Relative Humidity (percent)						Wind (miles per hr.)		
				Ave. daily max.			Ave. daily min.			Ave. daily max.			Ave. daily min.			Ave. daily velocity		
	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934
April	65	64	64	81	77	76	49	51	52	81	88	80	47	56	46	....	2.18	....
May	63	75	73	77	88	84	49	62	62	89	87	88	67	54	56	3.02	2.47	2.37
June	75	76	80	89	93	92	60	60	68	88	80	88	61	42	59	1.90	1.99	1.89
July	81	78	82	96	88	93	67	68	71	89	97	89	66	69	59	1.83	2.09	1.36
August	79	78	80	91	91	90	67	65	71	89	91	91	75	59	61	1.52	1.32	1.37
September	74	78	75	85	93	89	63	63	62	79	86	93	63	50	59	3.40	1.41	1.35
October	63	67	..	78	84	..	47	50	..	85	80	..	68	50	..	....	1.05	....
Growing season	73	74	75	85	88	87	62	61	64	84	88	88	64	54	56	2.53	1.78	1.78

RAINFALL AND EVAPORATION

In Table 2 are shown the rainfall data for 1932 to 1934 and the total rainfall for each growing season. In 1933 low rainfall occurred during June, August, September, October, and November. Only 2.96 inches of rain fell from September 4 to December 4. The greatest amount of rainfall occurred between April 3 and May 15. Another wet spell occurred in July. The rainfall for March, April, May, and July constituted nearly 76 percent of the total rainfall for the year. In 1934 the distribution of the rainfall was more or less normal. July had the highest total rainfall, while March, May, and September were months with low rainfall. The total rainfall for the months of May to September for the three years was highest in 1934 and lowest in 1932.

The evaporation data (measured with Livingston porous cup atmometers) for the five months (May to September) for 1932-1934 are shown in Table 2. The average daily evaporation rate during 1932 was highest in May and lowest in August. In 1933, June had the highest average daily evaporation and May had the lowest. In 1934 the average daily evaporation did not vary much from month to month. Apparently the growing season for 1933 was the driest, and that of 1934 was the most humid. In both rainfall and evaporation the extremes were less pronounced in 1934 than in 1933.

TABLE 2. RAINFALL AND EVAPORATION

Month	Rainfall			Average Daily Evaporation		
	1932	1933	1934	1932	1933	1934
	Inches			*Cubic centimeters*		
January	....	5.49	5.81	....	....	....
February	....	2.40	6.97	....	....	....
March	....	11.62	3.45	....	....	....
April	....	24.72	7.41	38.4	29.9	....
May	3.43	11.93	4.25	33.9	28.6	24.2
June	3.79	1.54	6.84	31.4	43.2	29.6
July	3.58	8.56	9.78	28.2	35.7	21.1
August	6.58	1.66	7.75	21.8	31.1	26.0
September	2.58	1.88	3.44	26.6	37.4	24.2
October	3.69	0.70	....	....	46.4	....
November	3.69	0.86	....	....	....	....
December	5.71	3.68	....	....	....	....
Total	32.97 (eight months)	75.04 (full year)	55.70 (nine months)	....	....	....
Total (May-September)	19.96	25.57	32.06	....	....	....
Average (May-September)	....	....	....	28.4	35.2	25.0

TREATMENT OF EXPERIMENTAL PLOTS

Three combinations of conditions were studied: (1) the effect of density of stocking on the rate of growth of longleaf pine seedlings; (2) the combined effect of the ground cover and density of stocking on the growth of the pine seedlings; and (3) the combined effect of the ground cover and the scrub oaks on the growth of the seedlings.

Seven plots were established in which all the oaks, herbs, and grasses were removed by hoeing, leaving on the bare ground only the selected pine seedlings, which were thinned to densities of 1, 5, 10, 15, 25, 50, and 100 seedlings per milacre. Seven more plots were laid out in which all the scrub oaks were removed, leaving only the pine seedlings and the grass and herbs; the stands of pine seedlings were thinned to the same densities as in the denuded plots. Thus, two conditions were established—in one the pine seedlings presumably competed among themselves, and in the other the pine seedlings presumably competed with each other and also with the grasses and herbs. The third condition was obtained by the establishment of one plot in which scrub oak, grasses, herbs, and pine seedlings were intermixed. This plot was left undisturbed, except for the thinning of the pine seedlings to a density of five to the milacre. The plots varied in size according to density of stocking, but 100 seedlings per plot constituted the minimum. Figure 2 shows approximately the area occupied by each pine seedling in the plots of the different densities.

During the first growing season after establishment, the denuded plots

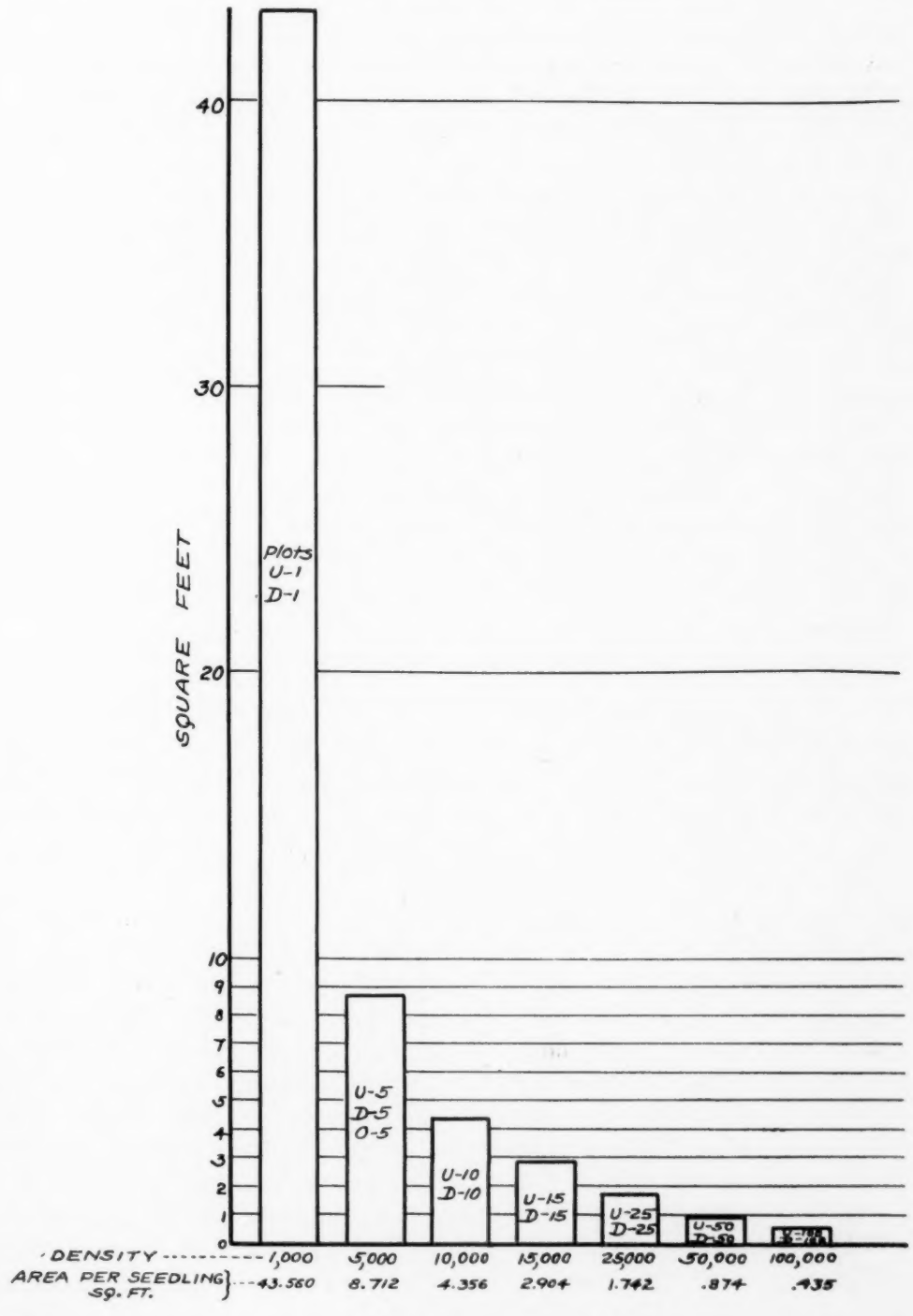

FIG. 2. Graphic presentation of surface area occupied by each pine seedling in different plots.

had to be weeded at monthly intervals, while during subsequent seasons two or three weedings per season were sufficient to keep out all weeds and grasses. The original denudation was accomplished by hoeing but after the first season only occasional herbs and grasses appeared on the denuded plots, and these were generally pulled out by hand.

In all of these plots the seedlings were selected as to uniformity of age, size, and condition of the terminal bud, and were as evenly spaced in the plots as possible. Each plot was surrounded by an isolation strip varying in width from 2 to 4 m., depending on the size of the plot. A trench was dug around each isolation strip to a depth of 76 cm. to cut off all of the roots from surrounding trees, herbs, and grasses; and each year this trench was remade. In each plot, as well as in the isolation strips, the seedlings were sprayed with Bordeaux mixture at monthly intervals during the growing season (and less frequently during the dormant season) to prevent infection from the brown-spot leaf blight. The seedlings within the plots were all tagged and measured as to height and diameter at the time of establishment of the plots and again at the end of each growing season. In Table 3 is shown the number of seedlings per plot and the treatment and designation of each plot.

MICRO-ENVIRONMENT

EVAPORATION

Livingston spherical porous clay cup atmometers were arranged in pairs (one black and one white) in each plot. The reservoir bottle of each atmometer unit was placed in the ground to its neck so that the center of the

TABLE 3. DENSITIES IN STANDS AND TREATMENTS OF PLOTS

Plot number[1]	PLOT		
	Density per acre	Number of seedlings studied	Area per seedling
	Thousands		*Square feet*
O5M	5	100	8.712
U1M	1	100	43.560
U5M	5	100	8.712
U10M	10	200	4.356
U15M	15	225	2.904
U25M	25	200	1.742
U50M	50	200	0.871
U100M	100	200	0.435
D1M	1	100	43.560
D5M	5	100	8.712
D10M	10	100	4.356
D15M	15	225	2.904
D25M	25	100	1.742
D50M	50	100	0.871
D100M	100	100	0.435

[1]Treatment:
O = Natural condition including oaks, herbs, grasses, and pine seedlings—oak plot.
U = Oaks removed; herbs, grasses, and pine seedlings retained—grass plots.
D = Oaks, herbs, and grasses removed; only pine seedlings retained—denuded plot.

evaporative surface of the cup was about 7.6 cm. above ground, and each unit was equipped with a mercury rain-correcting valve. The atmometers were placed so that they would not be shaded by tall trees or snags, but in the grass area it was not always possible to prevent some local shading.

TEMPERATURE

The maximum temperature at the soil surface (about 5 mm. below the surface) was determined by maximum thermometers, which were read each morning. In addition to the thermometers at the soil surface, maximum and minimum thermometers of the Sixe-incubator type were inserted horizontally so that the bulb was 12.7 cm. below the soil surface and the face of the thermometer was exposed in a wooden box with a lid. When readings were taken the lid of the box was removed, the temperature read, and the indicators moved back with a magnet; in this way the bulb of the thermometer was never disturbed. These thermometers were placed in the plots with the extreme densities and in the one with the intermediate density (plots with 1, 25, and 100 seedlings per milacre). In these plots the maximum and minimum temperatures were also read each morning from thermometers placed at 5 cm. above ground. Thus temperatures were obtained at three levels: at 12.7 cm. below the surface, at the surface, and at 5 cm. above the surface of the ground.

At weekly intervals during the growing season and at monthly intervals during the dormant season composite samples of soil were collected from each plot at three depths: 0-5 cm., 5-15 cm., and 15-30 cm. These samples were tested for pH by means of the quinhydrone electrode method, and the soil moisture was determined on oven-dry basis.

ROOT EXCAVATIONS

In order to determine the relationship between the roots of the pine seedlings and the density of stocking, an area was selected on which the site conditions were uniform and on which all the seedlings were of the same age. On this area two milacre quadrats were laid out. On one quadrat there were 24 longleaf pine seedlings, and on the other there were 185 seedlings of the same age. On both milacres the seedlings were in their thirteenth growing season. The vegetation consisted principally of pine forest grasses (*Andropogon scoparius* and *A. elliottii*) and a few legumes, the dominant among which was *Cracca virginiana*. Ruston fine sandy loam was the soil type on both milacres studied. The degree of the intensity of the brown-spot needle blight infection was similar on both quadrats and the seedlings showed indications of heavy periodic defoliation. The only apparently significant difference between the two milacre quadrats was in the number of pine seedlings.

The milacres were marked off and the vegetation on them was mapped. Along the full length of one side of each quadrat was dug a trench a little

over a meter in depth and a meter wide—large enough to permit the free movement of a person. The roots of the pine seedlings were then carefully excavated with an ice pick, measured, and sketched. After a seedling had been completely excavated, it was removed to the laboratory where it was mounted on a large paper marked off in 2½-cm. squares. The measurements of the roots of the seedling were then checked with those on the sketch made in the field, and the seedling was then photographed in the mounted position.

ANALYSIS OF DATA

TEMPERATURE

The average daily temperatures for the growing seasons of 1932, 1933, and 1934 combined are summarized in Table 4. The average maximum temperature at the soil surface was consistently higher in the denuded plots than in the grass plots, but the differences between the maximum temperature on the different plots with the same ground cover did not seem to be consistent.

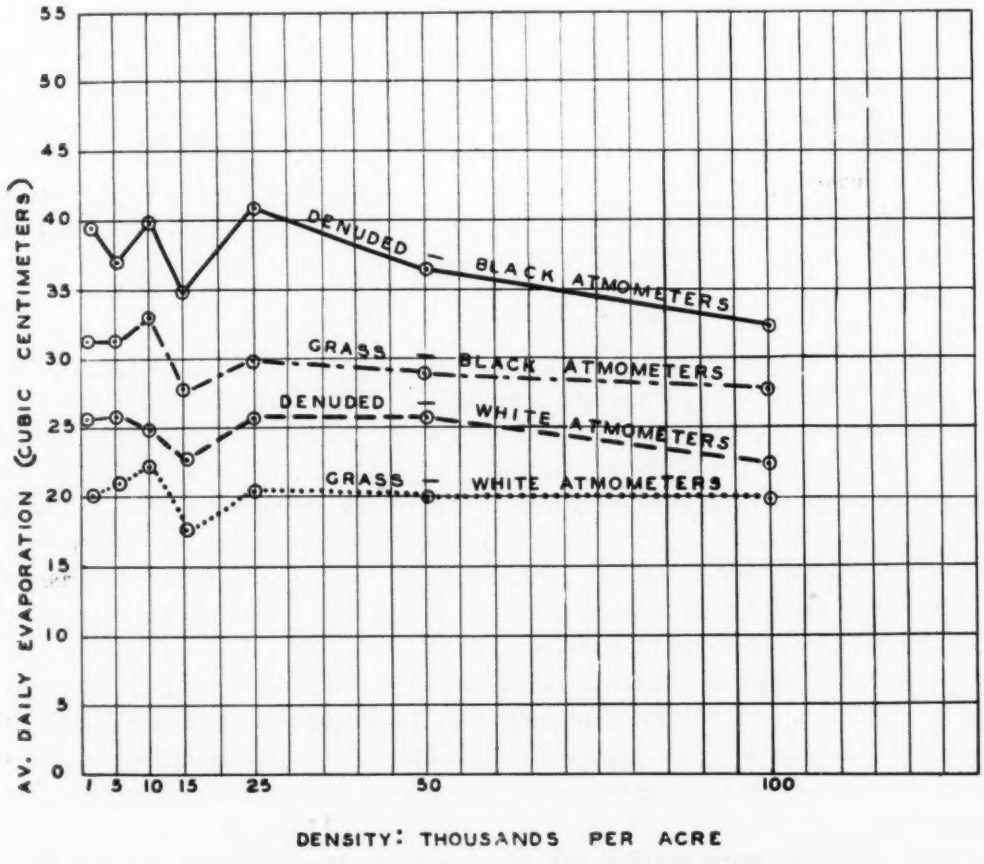

FIG. 3. Average evaporation in cubic centimeters for three growing seasons (1932-1934).

TABLE 4. AVERAGE DAILY MAXIMUM TEMPERATURE, AVERAGE DAILY EVAPORATION, AVERAGE SOIL MOISTURE, AND AVERAGE SOIL ACIDITY FOR THREE GROWING SEASONS (1932, 1933, AND 1934)

Density per acre	Condition of plot	Evaporation				Maximum Temperature						Soil Moisture (percent)						Soil Acidity (pH)					
		Atmometers										Depth (cm)						Depth (cm)					
		Black (cc)		White (cc)		Air (°F.)		Surface (°F.)		Below surface (°F.)		0-5		5-15		15-30		0-5		5-15		15-30	
		Average	Difference	Average	Difference	Average	Difference	Average	Difference	Average	Difference	Average	Difference	Average	Difference	Average	Difference	Average	Difference	Average	Difference	Average	Difference
1,000	Denuded	39.8	8.4	25.9	5.8	95.5	.....	100.7	8.6	86.1	.....	11.6	.....	12.1	.....	14.1	.....	5.1	0.1	5.1	.....	4.9	.....
	Grass	31.4	.....	20.1	.....	103.0	7.5	93.1	.....	86.8	0.7	14.2	2.6	14.1	2.0	16.6	2.5	5.0	.....	5.2	0.1	5.0	0.1
5,000	Denuded	37.4	5.9 10.7	26.0	5.0 4.0	....	.....	103.5	12.4 20.8	....	.....	11.3	.....	12.2	.....	14.1	.....	5.0	0.1 0.3	4.9	0.3 0.2	4.9	0.2 0.3
	Grass	31.5	.....	21.0	.....	.....	.....	91.1	.....	.....	.....	19.9	8.6 2.3	16.2	4.0 2.6	16.1	2.0 1.8	4.9	.....	4.6	.....	4.7	.....
	Oaks	26.7	.....	22.0	.....	.....	.....	82.7	.....	.....	.....	17.6	.....	13.6	.....	14.3	.....	4.7	.....	4.7	.....	4.6	.....
10,000	Denuded	40.1	6.7	25.3	2.7	.....	.....	104.9	15.1	.....	.....	11.2	.....	13.2	.....	14.8	.....	4.8	.....	4.9	.....	4.9	.....
	Grass	33.4	.....	22.6	.....	.....	.....	89.8	.....	.....	.....	15.9	4.7	13.2	.....	15.2	0.4	5.1	0.3	5.2	0.3	5.0	0.1
15,000	Denuded	34.9	6.7	23.2	5.3	.....	.....	107.2	20.1	.....	.....	12.4	.....	12.0	.....	13.8	.....	4.9	.....	4.9	0.1	5.0	.....
	Grass	28.2	.....	17.9	.....	.....	.....	87.1	.....	.....	.....	15.8	3.4	13.1	1.1	13.9	0.1	5.1	0.2	4.8	.....	5.2	0.2
25,000	Denuded	41.1	10.8	25.9	5.3	97.4	1.6	100.3	8.3	91.6	6.2	11.2	.....	11.8	.....	13.9	.....	4.8	.....	4.9	.....	4.9	0.2
	Grass	30.3	.....	20.6	.....	95.8	.....	92.0	.....	85.4	.....	16.8	5.6	14.6	2.8	14.9	1.0	4.9	0.1	4.9	.....	4.7	.....
50,000	Denuded	36.6	7.1	25.8	5.7	.....	.....	100.5	13.9	.....	.....	13.3	.....	13.8	.....	14.6	0.3	5.0	.....	4.8	.....	4.8	.....
	Grass	29.5	.....	20.1	.....	.....	.....	86.6	.....	.....	.....	16.9	3.6	13.8	.....	14.3	.....	5.0	.....	5.1	0.3	5.0	0.2
100,000	Denuded	32.5	4.2	22.5	2.6	98.4	.....	95.5	5.2	84.1	.....	14.8	0.4	14.2	0.6	15.7	0.6	4.7	.....	4.9	.....	4.8	.....
	Grass	28.3	.....	19.9	.....	100.2	1.8	90.3	.....	84.1	.....	14.4	.....	13.6	.....	14.9	.....	4.7	.....	5.1	0.2	4.8	.....

EVAPORATION

The data on the evaporation rate on the different plots are shown in Table 4 and Figure 3. It is at once evident that the average daily evaporation was greater in the denuded than in the grass plots, but there is no definite relationship between the evaporation rate and the density of stocking. Neither in grass plots nor in denuded plots does the evaporation rate vary much with the density. The increased evaporation rate in the denuded plots is probably caused by the higher light intensity and greater air movement than in the grass plots. These factors should also increase the transpiration from the pine seedlings, but apparently such an increase in transpiration did not have a harmful effect on the seedlings, for, as will be shown later, in all cases the seedlings in the denuded plots where the evaporation rate was higher showed a greater increase in growth than did the seedlings in the grass plots. The evaporation data seem particularly significant because they show the influence of ground cover on evaporation in the immediate vicinity of the pine seedlings.

LIGHT

The intensity of the light on the different plots was not measured directly but by using the difference in evaporation between the black and white atmometer cups as an expression of the solar radiation, a figure was obtained which suggests a strong correlation between the light intensity and the density in the stands on the different plots. Assuming that the denuded plot with fewest seedlings had the most favorable light conditions, then the difference between evaporation on the denuded and the grass plots of that density (1 seedling per milacre) probably was due to increased solar radiation on the denuded plot. This difference in evaporation was then taken as 100 percent

TABLE 5. DIFFERENCES IN THE AVERAGE DAILY EVAPORATION BETWEEN THE BLACK AND WHITE ATMOMETERS (SOLAR RADIATION)

Density per acre	Condition of plot	Difference in evaporation between black and white atmometers (cc)	Light Intensity (percent)		Oak plot
			Grass plot	Denuded plot	
1,000	Denuded	13.9	....	100	....
	Grass	11.3	81.3	....	....
5,000	Denuded	11.4	....	82	....
	Grass	10.5	75.5	....	....
	Oak	4.7	....	....	33.8
10,000	Denuded	14.8	....	106.5	....
	Grass	10.8	77.7	....	....
15,000	Denuded	11.7	....	84.2	....
	Grass	10.3	74.1	....	....
25,000	Denuded	15.2	....	109.3	....
	Grass	9.7	69.8	....	....
50,000	Denuded	10.8	....	77.7	....
	Grass	9.4	67.7	....	....
100,000	Denuded	10.0	....	71.9	....
	Grass	8.4	60.4	....	....

solar radiation. On this basis, the differences in evaporation between the denuded and the grass plots of the different densities were then computed to indicate the solar radiation on each plot. The data in Table 5 show that in the grass plots the light (solar radiation) definitely decreases with the density of the stand. In the denuded plot this is not as marked as in the grass plots.

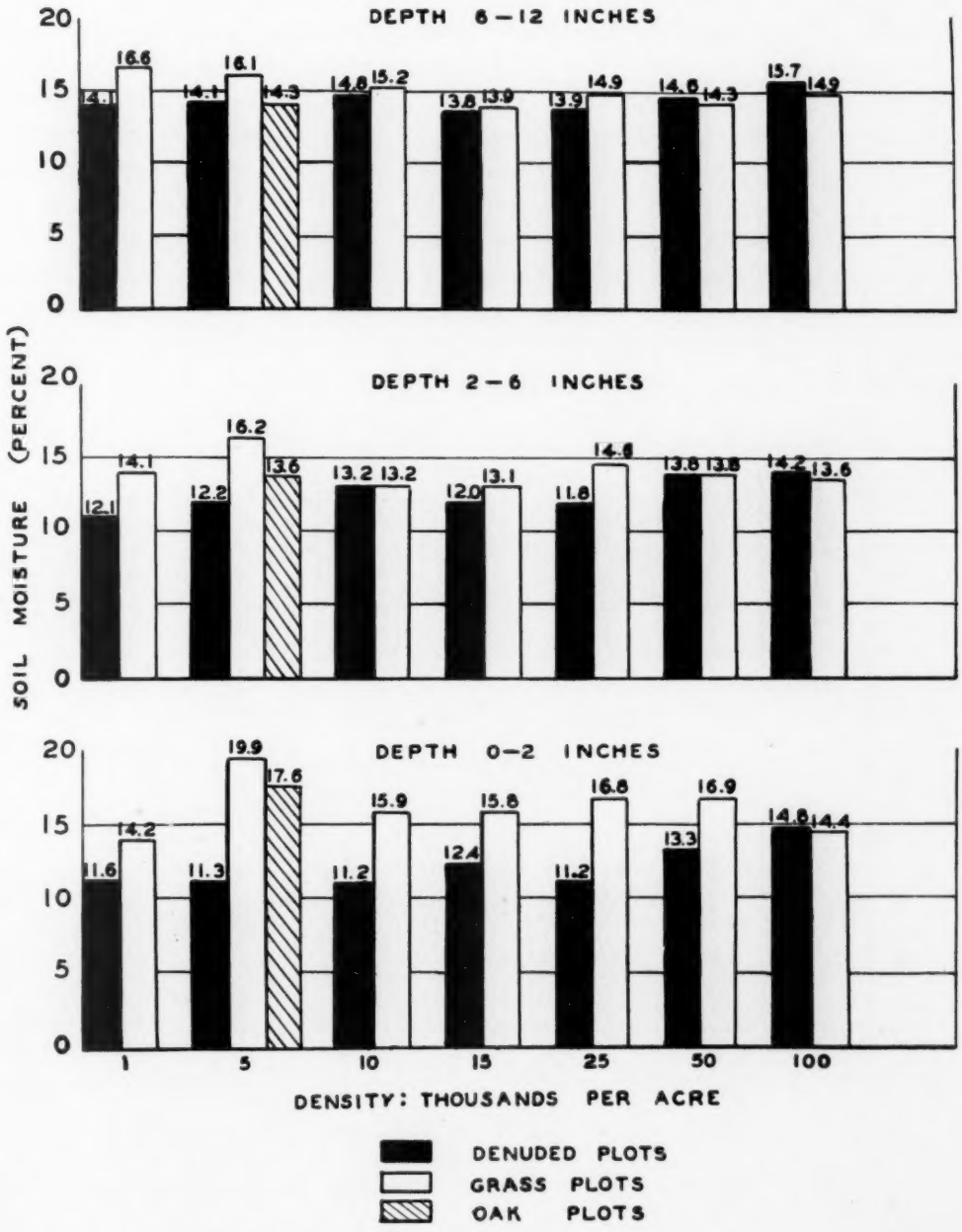

FIG. 4. Average soil moisture on dry weight basis for three growing seasons (1932-1934).

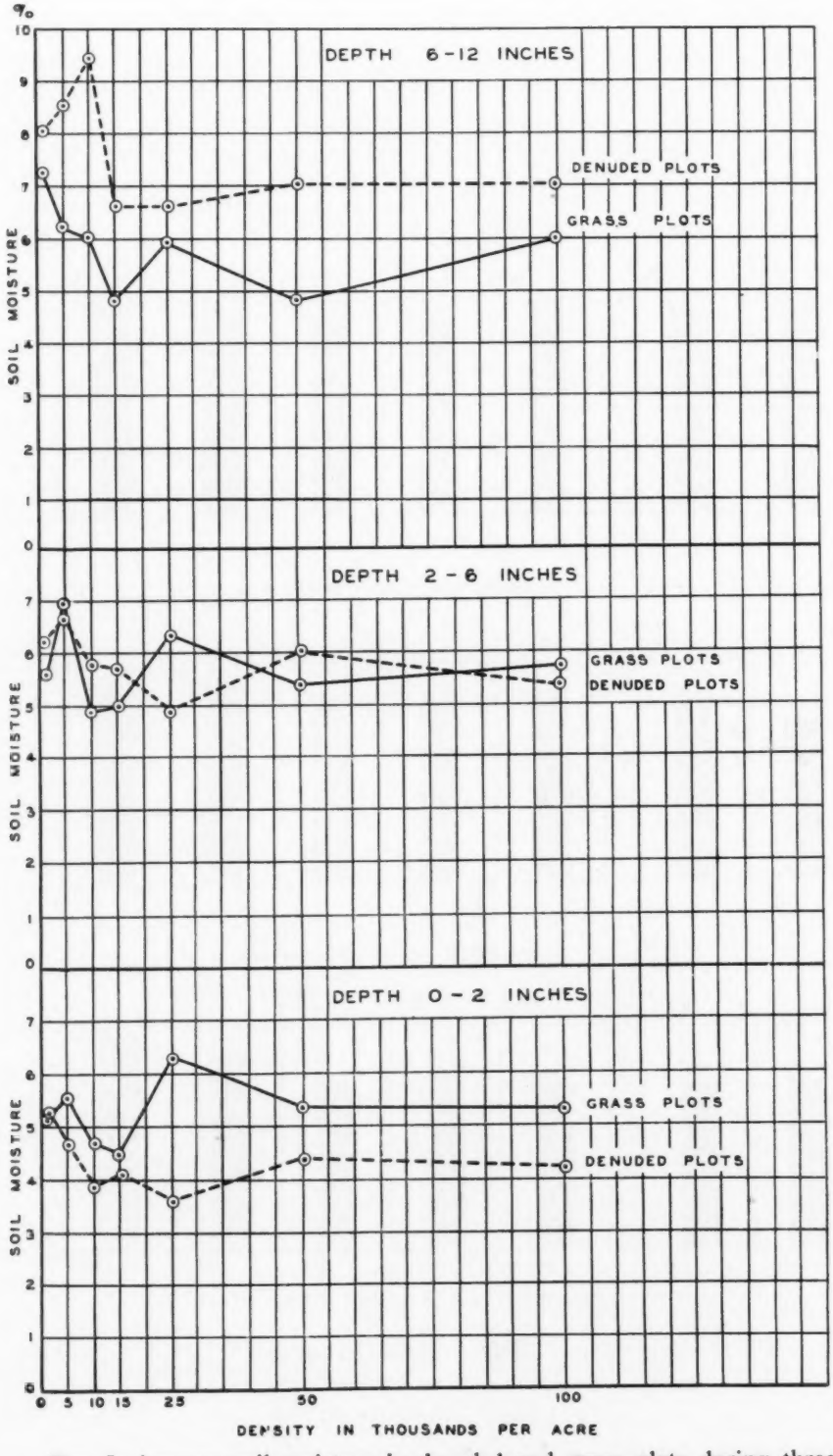

FIG. 5. Average soil moisture in denuded and grass plots during three months' drought—September 4 to December 4, 1933. Total rainfall 2.96 inches.

SOIL MOISTURE

Determinations of soil moisture of composite soil samples taken weekly from each plot during the three growing seasons (Table 4 and Fig. 4) showed that the average soil moisture was less at the surface layer (0-5 cm.) in all denuded plots than in the grass plots, except in the one with 100 seedlings per milacre, where the difference is very small. In the next depth (5-15 cm.), the results were not very consistent, although in general there appeared to be more moisture in the grass plots of the lesser densities than in the denuded plots of the same densities. The same can be said for the soil moisture at the lowest depth (15-30 cm.), although the differences tend to disappear with increasing densities. The differences at this depth between the denuded and the grass plots were very small.

Of particular interest are the data on soil moisture obtained during the period of low rainfall (September 4 to December 4, 1933) when the total rainfall for the 3 months amounted to only 2.96 inches. During this period (Table 6 and Fig. 5) all the grass plots except the one with the least density showed a higher moisture content near the surface than did the denuded plots, but at the lower depths this condition becomes reversed.

In general, the data seem to indicate that under normal conditions soil moisture is adequate for plant growth; the differences between soil moisture of the grass plots and that of the denuded plots are insignificant. A somewhat different condition prevails during a period of low rainfall when the water supply in the soil is low. Then the denuded plots show a slightly lower moisture content in the upper 5 cm. of soil than do the undenuded

TABLE 6. SOIL MOISTURE ON THE PLOTS DURING A PERIOD OF LOW RAINFALL (SEPTEMBER 4-DECEMBER 4, 1933)[1]

Density per acre	Condition of plot	Soil Moisture At Depths:					
		0-5 cm	Difference	5-15 cm	Difference	15-30 cm	Difference
		Percent					
1,000	Denuded	5.29	0.10	6.23	0.60	8.13	0.92
	Grass	5.19	....	5.63	....	7.21	....
5,000	Denuded	4.69	....	6.75	....	8.49	2.25 2.92
	Grass	5.63	0.94 0.04	6.92	0.17 2.16	6.24	....
	Oak	5.59	....	4.76	....	5.57	....
10,000	Denuded	3.94	....	5.66	0.73	9.40	3.40
	Grass	4.76	0.82	4.93	....	6.00	....
15,000	Denuded	4.14	....	5.72	0.76	6.58	1.77
	Grass	4.54	0.40	4.96	....	4.81	....
25,000	Denuded	3.60	....	4.91	....	6.61	0.71
	Grass	6.31	2.71	6.26	1.35	5.90	....
50,000	Denuded	4.38	....	5.98	0.69	6.96	2.12
	Grass	5.45	1.07	5.29	....	4.84	....
100,000	Denuded	4.25	....	5.44	....	7.07	1.07
	Grass	5.28	1.03	5.77	0.33	6.00	....

[1]The rainfall during these 3 months amounted to 2.96 inches.

plots, but the high moisture content of the soil in the denuded plots at a depth of 15-30 cm. is very marked. At 5-15 cm. the soil moisture curves are intermediate and rather irregular. At the surface, due to high evaporation, the soil moisture content is lower in the denuded plots than in the grass plots, while at 15-30 cm. the roots of the plants in the grass plots draw moisture from the lower depths; when water is plentiful they obtain enough water from the 5-15 cm. level. In the denuded plots, however, both evaporation and the loss of moisture through the seedlings account for the low water content above 15 cm., but the drain on the moisture below 15 cm. is not as heavy as in the grass plots. These data seem to indicate that the competition between grasses and pine seedlings for water is greater when moisture in the soil is low than when the soil contains a sufficient amount of moisture. Scrub oaks, however, seem to exert keen competition for moisture, as is shown by the low moisture content in the lower depths of soil both under normal weather conditions and during droughts.

RESPONSE OF PINES TO DENUDATION AND THINNING

The effect of denudation on the rate of growth of longleaf pine seedlings, which for 12 years had been growing very slowly, was very rapid. Even after one growing season the response was very obvious. The seedlings in the denuded plot with the lowest density (1 per milacre) showed an increase in height in one growing season of over 456 percent. The other denuded plots likewise showed marked increases (Table 7).

After three growing seasons this response was particularly noticeable. There obviously exists a definite correlation between density of the stand and rate of growth of the seedlings. This is especially evident in the denuded plots where the ground cover has been removed in all cases and where the density alone varied. There we find for all height classes the increase in growth is progressively smaller as the densities become greater (Table 8 and Fig. 6).

TABLE 7. PERCENTAGE OF INCREASE IN HEIGHT GROWTH OF LONGLEAF PINE SEEDLINGS IN ONE GROWING SEASON AFTER ESTABLISHMENT OF PLOTS

Density per acre	Condition of plot	Percent increase in height growth
1,000	Denuded	456
	Grass	64
5,000	Denuded	115
	Grass	46
	Oak	0
10,000	Denuded	79
	Grass	33
15,000	Denuded	56
	Grass	31
25,000	Denuded	57
	Grass	23
50,000	Denuded	15
	Grass	27
100,000	Denuded	25
	Grass	18

TABLE 8. SUMMARY OF HEIGHT GROWTH OF TREES ON ALL PLOTS

Density per acre	Condition of plot	Original Height Class (in feet)																						Areas per plot (milacres)
		0.10 (3 cm.)				0.20 (6 cm.)				0.30 (9 cm.)				0.40 (12 cm.)				0.60 (18 cm.)				All classes				
		Number of trees	Average height		Percent increase	Number of trees	Average height		Percent increase	Number of trees	Average height		Percent increase	Number of trees	Average height		Percent increase	Number of trees	Average height		Percent increase	Number of trees	Average height		Percent increase	
			1932	1935			1932	1935			1932	1935			1932	1935			1932	1935			1932	1935		
1,000	Denuded	56	.12	3.27	2,625	38	.17	4.65	2,579	4	.30	6.37	1,990	.....	.....	.....	.....	2	.6	10.10	1,583	98	[1].15	3.16	2,007	100
	Grass	90	.10	.70	600	9	.17	1.67	882	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	99	.11	.80	627	100
5,000	Denuded	82	.13	2.22	1,608	18	.18	2.78	1,444	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	100	.13	2.32	1,685	20
	Grass	83	.12	.55	358	15	.17	.83	388	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	98	.12	.58	383	20
	Oak	66	.11	.22	100	33	.20	.37	85	1	.28	.70	150	.....	.....	.....	.....	.....	.....	.....	.....	100	.15	.27	80	20
10,000	Denuded	60	.12	.98	718	37	.17	1.07	529	1	.27	.80	196	.....	.....	.....	.....	.....	.....	.....	.....	98	.14	1.01	621	10
	Grass	180	.11	.40	263	16	.18	.86	377	2	.30	1.55	417	.....	.....	.....	.....	.....	.....	.....	.....	198	.12	.45	275	20
15,000	Denuded	106	.10	.81	710	109	.18	1.09	506	8	.28	1.52	443	1	.36	3.10	761	.....	.....	.....	.....	223	[2].16	.97	506	15
	Grass	191	.12	.37	208	30	.18	.58	222	3	.29	.77	166	.....	.....	.....	.....	.....	.....	.....	.....	224	.13	.40	208	15
25,000	Denuded	59	.12	.73	425	39	.18	.80	344	1	.26	3.40	1,208	.....	.....	.....	.....	.....	.....	.....	.....	99	.14	.78	457	4
	Grass	174	.12	.27	125	30	.19	.39	105	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	204	.13	.29	123	8
50,000	Denuded	80	.12	.38	217	20	.17	.56	229	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	100	.13	.42	223	2
	Grass	180	.11	.20	91	17	.18	.33	94	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	196	.11	.21	91	4
100,000	Denuded	94	.12	.29	141	8	.18	.54	200	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	102	.12	.31	158	1
	Grass	194	.10	.20	100	7	.18	.36	100	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	203	.11	.20	82	2

[1]The 18-cm. class excluded from computations.
[2]The 12-cm. class excluded from computations.

There also appears to be a definite relationship between original height of the seedling and increase in growth. The percentage of increase in growth in the denuded plots was generally greater for seedlings whose original height class was 3 cm. than for those whose original height class was 6 cm., while in the grass plots the reverse seems to be true; the smaller seedlings generally made less growth than the taller seedlings.

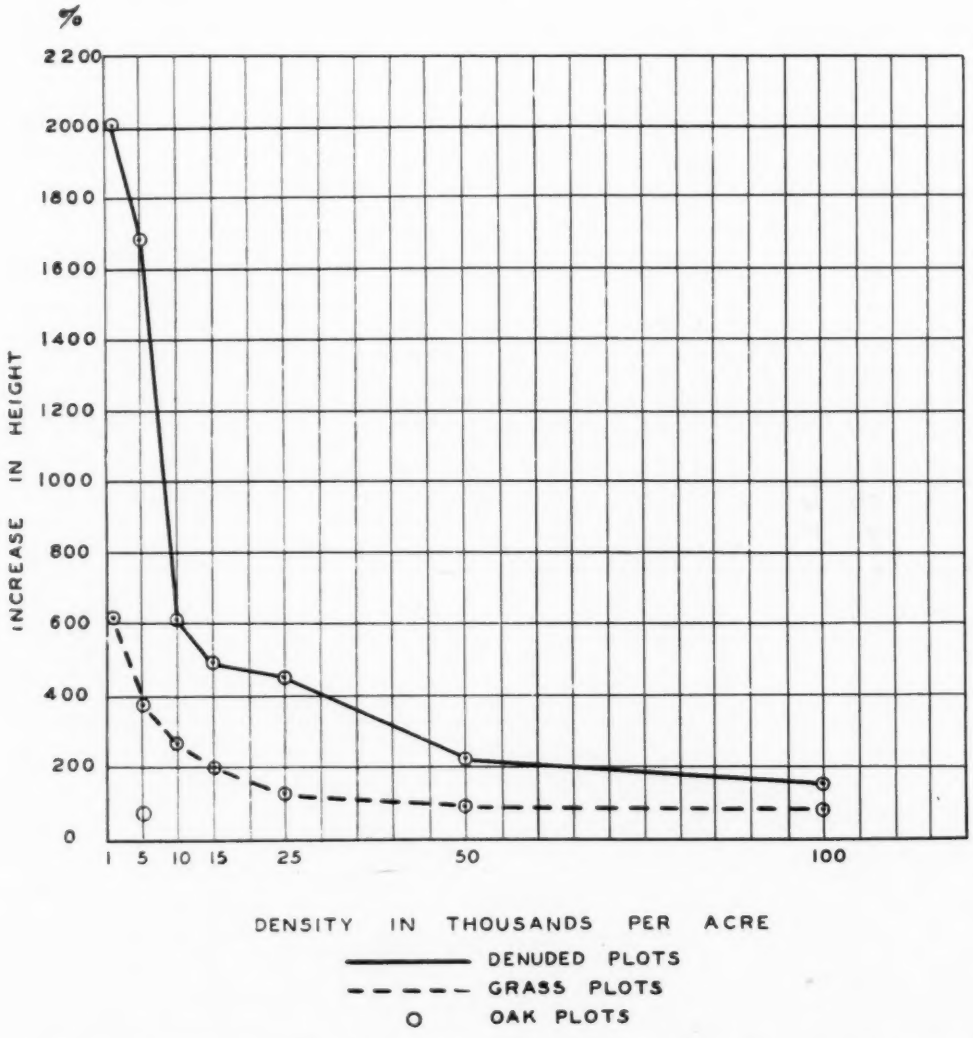

FIG. 6. Increase in height during growing seasons of 1933-1935. Combined 0.10, 0.20, and 0.30 ft. classes.

The combined effect of density and ground cover on the growth of longleaf pine seedlings is just as pronounced. A study of Figure 6 and Table 8 shows that the average increase in growth in the grass plots was much smaller than in the denuded plots, indicating that the ground cover in the grass plots caused retardation of the growth of the seedlings. The most

spectacular increase in growth took place in the denuded plot with the density of one seedling per milacre, where the growth showed an increase of 2,007 percent as against 627 percent in the grass plot. In other words, the difference in the increase in growth between the seedlings in the denuded and those in the grass plots apparently was related to the removal of the ground

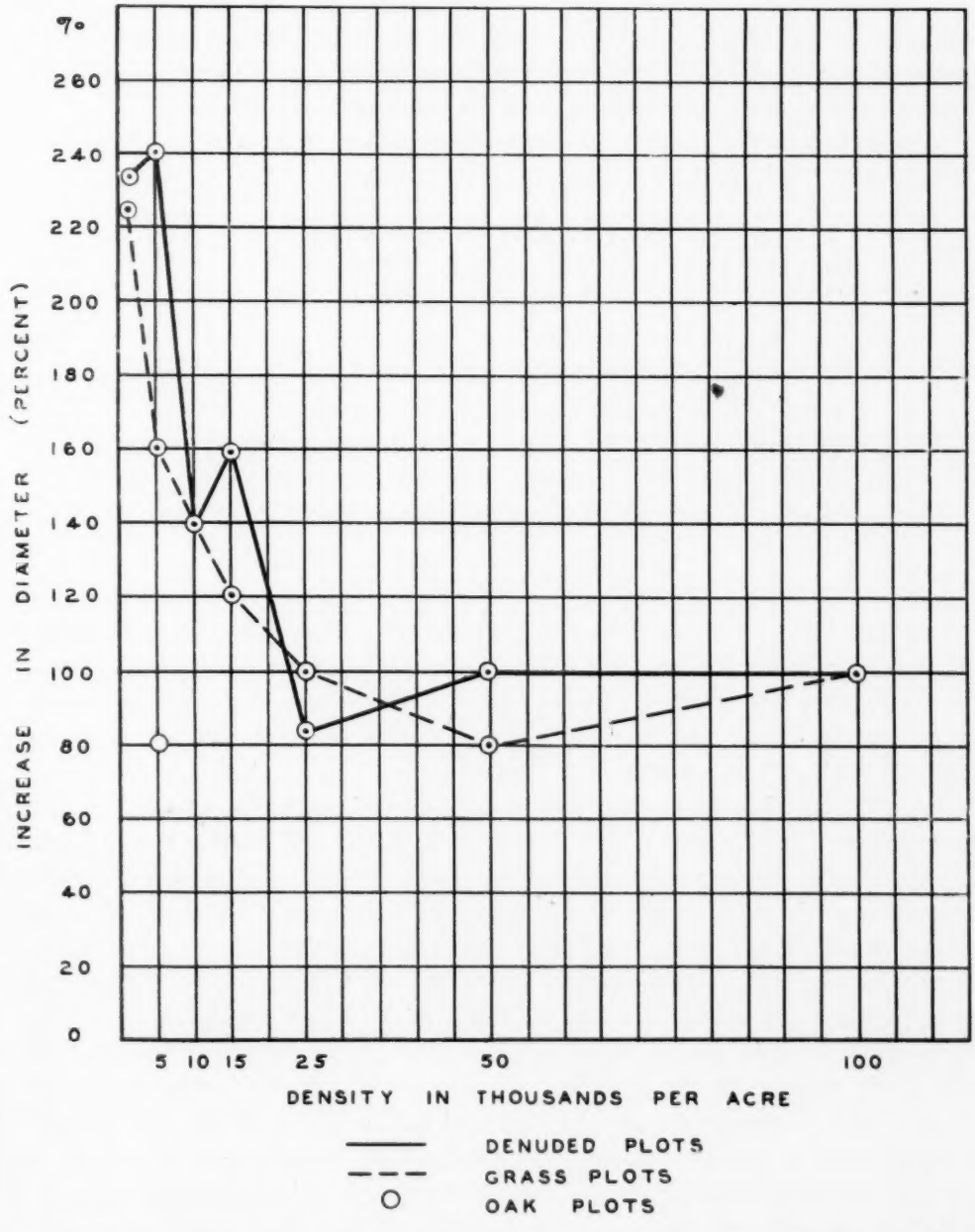

FIG. 7. Increase in diameter of seedlings during growing seasons 1933-1935. Original diameter class 0.3 to 0.9 inch.

cover. The ratios of the increase in growth for the three growing seasons in the denuded plots to that in the grass plots run as follows.

	Thousand Seedlings Per Acre						
Density	1,000	5,000	10,000	15,000	25,000	50,000	100,000
Ratios	4.4:1	4.8:1	2.6:1	3.0:1	4.0:1	2.9:1	2.1:1

The effect of density on stem diameter at the ground level can be seen in Table 9 and Figure 7. In general, the seedlings in the denuded plots made greater growth in diameter than those in the grass plots, but the differences are in some cases too small to justify definite conclusions.

The ratios of the increase in diameter growth of the seedlings in the denuded plots to that in the grass plots are as follows:

	Thousand Seedlings Per Acre						
Density	1,000	5,000	10,000	15,000	25,000	50,000	100,000
Ratios	1.6:1	1.5:1	1:1	1.3:1	1:1	1.2:1	1.2:1

From these ratios it is seen that the effect of density and ground cover on the growth in diameter at the root collar of the pine seedlings is not very evident during the three growing seasons following the treatments.

Of particular interest is the fact that in the plot where the scrub oaks were left undisturbed, the seedlings showed the least growth in height, amounting to only 80 percent in two growing seasons.

DISCUSSION

To summarize, it may be stated that the measurements of the seedlings for three growing seasons following the establishment of the experiment show markedly the effects of both density of stocking and the ground cover on the height-growth of the seedlings. The data seem to indicate that the height-growth of the seedlings in the denuded plots, where the seedlings compete among themselves and where the competition varies in degree with the number of seedlings per acre, is markedly influenced by this competition. The plots with the larger number of seedlings showed a smaller increase in growth than those with smaller numbers of seedlings. The vegetation on the ground apparently acts as a keen competitor, for in the grass plots the growth in height is much less than in the denuded plots, where the ground cover has been removed. Marked evidence of the competition produced by the ground cover is seen in the scrub-oak plot where very little growth has been made during the two growing seasons following the establishment of the plot. One striking fact should be noted here: Many of the trees in the denuded plots in the densities of 1, 5, and 15 thousand per acre possessed fascicles with four and five leaves in each cluster. That is particularly significant, for generally seedlings possess fascicles of two leaves each, and only the more vigorous seedlings possess fascicles with three leaves each. Apparently, denudation has increased not only the height growth but also the

TABLE 9. SUMMARY OF DIAMETER GROWTH OF TREES ON ALL PLOTS

Density per acre	Condition of plot	Original Diameter Class (in inches)																			Area per plot (milacres)
		0.3				0.6				0.9				1.2 and above				All classes			
		Number of trees	Average diameter		Percent increase	Number of trees	Average diameter		Per cent increase	Number of trees	Average diameter		Per cent increase	Number of trees	Average diameter		Percent increase	Number of trees	Average diameter		Percent increase	
			1932	1935			1932	1935			1932	1935			1932	1935			1932	1935		
1,000	Denuded	4	0.3	2.0	567	78	0.6	2.0	233	15	0.7	2.2	214	3	1.0	2.6	160	100	0.6	2.0	233	100
	Grass	12	0.2	1.2	500	87	0.5	1.3	160	.....	.....	.....	.....	.....	.....	.....	.....	99	0.4	1.3	222	100
5,000	Denuded	4	0.3	1.6	433	93	0.5	1.7	240	3	0.7	2.0	186	.....	.....	.....	.....	100	0.5	1.7	240	20
	Grass	0	.....	.....	.....	91	0.5	1.3	160	7	0.7	1.5	114	.....	.....	.....	.....	98	0.5	1.3	160	20
	Oak	8	0.3	0.7	133	76	0.5	0.9	80	16	0.7	1.1	57	.....	.....	.....	.....	100	0.5	0.9	80	20
10,000	Denuded	6	0.3	0.9	200	86	0.5	1.1	120	6	0.7	1.4	100	.....	.....	.....	.....	98	0.5	1.2	140	10
	Grass	3	0.3	0.8	166	182	0.5	1.2	140	13	0.7	1.4	100	.....	.....	.....	.....	198	0.5	1.2	140	20
15,000	Denuded	4	0.3	1.1	266	204	0.5	1.3	160	17	0.7	1.4	100	.....	.....	.....	.....	225	0.5	1.3	160	15
	Grass	2	0.3	0.8	166	216	0.5	1.1	120	8	0.7	1.2	71	.....	.....	.....	.....	226	0.5	1.1	120	15
25,000	Denuded	3	0.3	1.0	233	78	0.5	1.1	120	17	0.8	1.4	75	.....	.....	.....	.....	98	0.6	1.1	83	4
	Grass	0	.....	.....	.....	186	0.6	1.0	67	14	0.7	1.2	71	.....	.....	.....	.....	200	0.5	1.0	100	8
50,000	Denuded	2	0.2	1.0	400	96	0.5	1.0	100	2	0.7	1.2	71	.....	.....	.....	.....	100	0.5	1.0	100	2
	Grass	6	0.3	0.8	166	186	0.5	0.9	80	5	0.7	1.1	57	.....	.....	.....	.....	197	0.5	0.9	80	4
100,000	Denuded	1	0.3	0.5	67	96	0.5	1.0	100	5	0.7	1.2	71	.....	.....	.....	.....	102	0.5	1.0	100	1
	Grass	5	0.3	0.7	133	198	0.4	0.8	100	.....	.....	.....	.....	.....	.....	.....	.....	203	0.4	0.8	100	2

vigor of the plants. The effect of density and ground cover on the growth in diameter at the root collar is as yet not marked, and the differences in growth in diameter between the seedlings in the denuded plots and those in the grass plots are too small for any conclusions. Another interesting fact is that in the denuded plots with densities of 1, 5, and 10 seedlings per milacre, six seedlings were found bearing pistillate cones on the uppermost branches (Pessin 1936). Four of these were only 1 foot in height and were already bearing pistillate cones, while one was 4 feet high and another 6 feet high.

The stand of pine seedlings on the area selected for the experiment was very heavy, in places as much as 435 to the milacre. Up to the time of the initiation of this study most of the seedlings which were 12 years old were badly infected with the brown-spot leaf blight and all were stunted, so that very few were over 5 cm. in height. The terminal buds were poorly developed on all of them and there were no indications of approaching height growth such as is known in longleaf pine seedlings when the terminal buds assume the characteristic candle-like appearance. To eliminate the factor of disease, all the seedlings were sprayed with Bordeaux mixture and nearly all the leaf blight disappeared by the end of the first growing season after establishment of the plots. The denudation was accomplished initially by hoeing, which during the first season had to be done several times to eliminate the sprouts of the perennials, but in the subsequent growing seasons light hoeing once or twice in the spring of the year usually removed any annuals that had started. Contrary to current belief, longleaf pine seedlings when cut at the surface of the ground sprout out again; it was, therefore, necessary to go over the plots three times during the first season and twice during the second season to eliminate the sprouts from the longleaf pine seedlings which were cut out during the establishment of the experiment. The removal of the oak sprouts did not offer a problem. It was found that when the scrub oaks were cut down in the spring after they were all in full leaf, they usually did not sprout profusely. Although an occasional oak stump would sprout, such juvenile twigs were easily removed, but those oaks which were cut down late in autumn or in winter required periodic removal of the sprouts.

A review of the data reveals that the average evaporation rate was consistently higher in the denuded plots than in the grass plots, but the differences under the same condition of ground cover did not vary significantly from plot to plot (density to density). The solar radiation (measured by the difference in evaporation between the black and white atmometers) was of course higher in the denuded than in the grass plots. The factors which influenced evaporation in the plots also influenced transpiration of the pine seedlings, but no evidence was anywhere present that such increased transpiration had a harmful effect on the pine seedlings. On the contrary, the seedlings in the denuded area showed greater vigor and growth than did those in the grass plots, where conditions for transpiration were less favorable.

Of particular interest is the temperature at the soil surface. In all the plots the average maximum temperature at the surface was considerably higher in the denuded plots than in the grass plots. Although the difference in the average maximum soil-surface temperature sometimes reached as much as 20°, no seedling was found in the denuded or the grass plots where the root collar showed any indication of injury.

The moisture content of the soil in the plots with the different densities did not vary markedly. It is true that the average moisture content of the soil during the three growing seasons was consistently higher in the upper 5 cm. of the soil in the grass plots, except in the plot with highest density, but in the lower depths the data were not consistent. At 15-30 cm. the soil moisture was somewhat higher in the grass plots with densities of 1 to 25 seedlings per milacre, while in the plots with densities of 50 and 100 seedlings per milacre the denuded plots showed somewhat higher moisture content than the grass plots. It is doubtful whether under normal conditions, with an average annual rainfall of over 65 inches, the soil moisture even under the most severe conditions of competition affects the growth of plants. During periods of low rainfall, however, such as existed from September 4 to December 4, 1933, the moisture content of the soil must influence the rate of competition for moisture among plants. The data at hand seem to bear this out. During these 3 dry months, the average soil moisture was lower in the surface layer of the denuded plots than in the grass plots, but the moisture was higher at the lower depth in the denuded plots than in the grass plots, indicating that the roots of the grasses were drawing upon the supply of moisture which would normally be utilized by the pine seedlings. Inasmuch as the drought occurred late in the growing season, however, it is doubtful whether this reduced supply of moisture in the lower depths seriously affected the growth of the pine seedlings.

Both the density of stocking and the denudation doubtless influenced the rate of growth of the pine seedlings in the different plots. The results are clear-cut and definite. These seedlings which were growing in the plots denuded of all vegetation made a phenomenal increase in growth within the brief period of three growing seasons. Even the seedlings with a density of 100 per milacre showed a considerably higher increase in growth than did those in the grass plot with the same density. The greatest growth occurred in the denuded plots with densities of 1, 5, 10, and 15 seedlings per milacre. That the removal of the grass stimulated the growth of the pine seedlings seems obvious, but no data are as yet available which might explain fully this phenomenal growth in the denuded plots.

The effect of the number of seedlings per milacre on the rate of growth of the pines is also very definite. Those crowded the most (100 per milacre) showed least increase in growth, while those in the plot with the lowest density showed the greatest increase.

It is safe to conclude that the ground cover has definitely been an influence in the retardation of growth of the seedlings, but the explanation for this is not so evident. On the basis of the results, one might be tempted to ascribe the cause to the removal of competition from the grass and herbs. But "competition" is an all-inclusive term and is meaningless unless the different factors operating during competition are definitely known. In this case, competition for moisture can be ruled out as an explanation for the slower growth of the pines in the grass plots, for at no time has the moisture content of the soil been critically low. Of particular interest is the fact that in the denuded plots with densities of 1, 5, 10, and 15 seedlings per milacre many trees have fascicles with four and five leaves each. This is especially true of the current growth (1936). Fascicles with two leaves are extremely rare and fascicles with three and four leaves are quite common; while in the grass plots the fascicles usually bear two and three needles per cluster.

Another point of interest is the apparent effect of denudation on cone production. In the denuded plots seedlings as low as 30 cm. were already bearing ovulate cones, which, however, died about June 5; but the fact that such low longleaf pine trees were already bearing cones, while other trees 20 times as high and of the same age were not bearing, is a question that needs further investigation.

ROOT STUDIES

The relationship between the root systems of the pine seedlings growing under different degrees of density (Pessin 1935) is of interest in connection with this study. The measurements of the excavated pine roots in plots with different densities are shown in Tables 10 and 11 and in Figure 8. The height of the excavated seedlings in the milacre with 185 seedlings varied from 0.6 to 3.1 inches, averaging 1.5 inches, whereas the length of the tap-

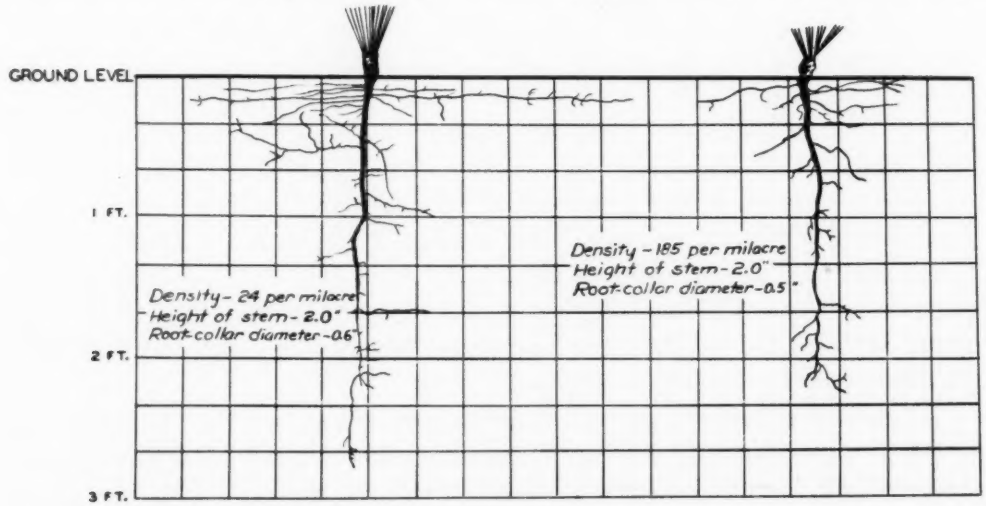

FIG. 8. Roots of longleaf pine seedlings 13 years old grown under same site conditions but in stands of different densities.

roots varied from 15.8 to 4.8 feet, averaging 2.3 feet, or about 18 times greater than the average length of the stem. Seedlings averaging 1.5 inches in height had an average total length of lateral roots of 5.4 feet and an average number of 26 lateral roots.

The height of the pine stems in the quadrat with the 24 seedlings per milacre varied from 0.98 to 4.02 inches, averaging 1.97 inches for the 21 seedlings excavated; whereas the length of the taproot varied from 1.3 to 5.5 feet, averaging 2.8 feet, or about 17 times greater than the average length of the stem. The average seedling, 1.97 inches in height, had an average total length of lateral roots amounting to 7.3 feet, with an average number of 31 lateral roots.

When the 19 seedlings excavated in the milacre with 185 seedlings were arranged by height classes, 10 seedlings fell in the 1.0-inch class, 7 in the 2.0-inch class, and 2 seedlings in the 3-inch class. The average length of the taproot for the first class was 25 times the length of the stem, for the second class 15 times, and for the third class 9 times the length of the stem, indicating that the ratio of the length of taproot to that of the stem decreases as the stem increases in height. The number of the lateral roots became greater

TABLE 10. ROOTS OF LONGLEAF PINE SEEDLINGS
Location: Bogalusa, Louisiana. Density: 185 seedlings per milacre. Age: 13 years.

Height of seedlings	Diameter of seedlings	Length of taproot	Number of lateral roots	Total length of lateral roots	Depth of occurrence of most lateral roots
Inches	*Inches*	*Feet*		*Feet*	*Feet*
0.6	.3	1.3	9	.8	.7
1.0	.5	2.8	16	3.8	.7
1.0	.5	3.2	22	4.5	.3
1.0	.6	2.3	41	6.0	.5
1.0	.4	1.3	15	1.7	.7
1.0	.5	3.0	47	11.4	1.0
1.1	.4	2.8	22	4.6	.7
1.1	.3	0.6	13	3.4	.7
1.4	.3	1.3	9	.6	.7
1.4	.5	2.2	23	2.7	.7
1.8	.5	1.3	11	.6	.7
1.8	.6	3.3	18	3.0	.7
2.0	.4	4.8	29	7.0	.7
2.0	.4	1.8	21	5.3	.8
2.0	.5	2.2	31	5.3	.5
2.1	.4	1.9	44	5.1	1.0
2.2	.7	2.5	41	10.5	.3
2.7	.6	1.7	31	9.2	1.7
3.1	.8	2.9	44	17.8	1.0
Average:					
1.5	.5	2.3	26	5.4	.7
Height class	Number of trees	.....	Average	.....	
Inches		*Feet*		*Feet*	*Feet*
1.0	10	2.1	22	3.9	.6
2.0	7	2.5	28	5.2	.7
3.0	2	2.3	37	13.5	1.3

as the height of the stem increased. The average number of lateral roots for the 1-inch class was 22; for the 2-inch class, 28; and for the 3-inch class, 37. The total length of the lateral roots also showed a definite relationship to size of stem. The lateral roots of the pine seedlings in the first class showed an average total length of 3.9 feet, those of the second class 5.2 feet, and those of the third class 13.5 feet.

TABLE 11. ROOTS OF LONGLEAF PINE SEEDLINGS
Location: Bogalusa, Louisiana. Density: 24 seedlings per milacre. Age: 13 years.

Height of seedlings	Diameter of seedlings	Length of taproot	Number of lateral roots	Total length of lateral roots	Depth of occurrence of most lateral roots
Inches	*Inches*	*Feet*		*Feet*	*Feet*
3.0	.8	2.2	59	11.2	.3
1.5	.4	2.2	33	3.8	1.3
1.5	.5	1.5	27	3.8	.8
2.0	.6	2.0	40	6.3	.8
4.0	.7	4.9	55	9.0	2.0
1.7	.6	2.7	22	9.6	1.0
4.0	.6	5.2	36	9.5	.5
1.7	.6	2.1	22	8.9	1.5
2.0	.5	3.7	19	8.8	.3
2.0	.6	2.7	40	9.2	.7
2.0	.6	2.5	31	9.7	1.0
1.6	.7	2.5	36	7.3	.5
2.0	.4	1.9	22	3.8	1.0
1.0	.4	2.3	12	0.8	0.3
1.5	.5	3.3	16	6.3	0.3
1.8	.6	2.3	33	10.6	2.0
1.8	.6	5.5	41	11.2	0.6
2.0	.5	3.5	25	5.6	2.0
1.9	.6	1.3	28	5.0	0.7
1.2	.5	2.8	22	4.5	1.0
1.7	.6	2.3	34	8.3	1.6
Average:					
2.0	.6	2.8	31	7.3	1.0
Height class	Number of trees	.....	Average	.....	
Inches		*Feet*		*Feet*	*Feet*
1.0	5	2.4	22	3.8	.7
2.0	13	2.7	30	8.0	1.5
3.0	1	2.2	59	11.2	.3
4.0	2	5.0	45	9.3	1.3

When the 21 seedlings from the low-density quadrat were arranged in height classes (Table 11), here, also, the number of lateral roots was proportional to size of seedlings, but whereas in the dense quadrat most of the seedlings fell in the 1-inch class, here most of the seedlings fell in the 2-inch class. This indicates that the density of the stocking had a retarding effect not only on the growth of the stems but also on the development of the root system, which in both the pine seedlings and the grasses is limited mainly to the top 30 cm. of soil.

SUMMARY

1. Experimental plots were established in 1932 in southeastern Louisiana in an area occupied by 12-year-old longleaf pine seedlings which were still in the grass and showed no evidence of height-growth.

2. The objects of the experiment were to determine the effect of the density of stand and the effect of ground cover on the rate of growth of the pine seedlings.

3. Altogether 15 plots were established. Seven plots with densities of 1, 5, 10, 15, 25, 50, and 100 seedlings per milacre were denuded of all herbaceous cover, shrubs, and other trees. Seven plots were thinned to the same densities and the herbaceous cover was left undisturbed, but the scrub oaks were removed. In the last plot all the herbaceous cover and the scrub oaks were left undisturbed and the seedling stand thinned to five pines per milacre. Each of these plots was surrounded by isolation strips, and a trench to eliminate roots from outside the plot was dug around each isolation strip. The seedlings in each plot were measured at the time of the establishment of the experiment and again at the end of each growing season.

4. Weekly records were taken of evaporation on each plot at 7.6 cm. above the surface of the ground. Samples for soil-moisture determination were also taken weekly at depths of 0-5 cm., 5-15 cm., and 15-30 cm.

5. Temperatures were recorded for the whole area by a Friez hygrothermograph placed 60 cm. above the ground. Maximum temperatures were also recorded daily during the growing season at 5 cm. above the ground, at the soil surface, and at 12.7 cm. below the surface of the soil.

6. The average soil moisture during the three growing seasons seemed consistently higher at the surface in the grass plots than in the denuded plots, except in the plots of greatest density, where the grass plot showed a soil-moisture content slightly less than the denuded plot. At 5-15 cm. the differences in soil moisture between the denuded and the grass plots were not consistent. At 15-30 cm. the soil moisture was somewhat higher in the undenuded plots that were least dense, whereas in the plots with the high densities (50 and 100 per milacre) the denuded plots showed a somewhat higher moisture content than the undenuded plots.

During a drought the average moisture content of the soil at 0-5 cm. below the surface was higher in the grass plots than in the denuded ones, but at 15-30 cm. the denuded plots showed a consistently higher moisture content than the grass plots.

7. The results indicate that as the density increased the growth in height of the seedlings during three growing seasons definitely decreased both in the denuded and in the grass plots.

8. The average increase in height growth of the longleaf pine seedlings in the denuded plots was greater under all densities than in the grass plots. The average increase in height in plots with 1 and 5 per milacre was nearly

five times that in the grass plots of the same density. Even in plots with the highest density (100 per milacre), the increase in growth was twice as much on the denuded plots as on the grass plots.

9. Roots of seedlings of longleaf pine in their thirteenth growing season were excavated in two milacres, in which the densities were 185 and 24 seedlings per milacre. Measurements of the roots indicate that the density of stocking not only influences the growth-rate of the stem, but also the growth-rate of the root system. It is also evident that during the few years following germination, the growth of the taproot is much more rapid than that of the stem. After height growth commences, the growth of the taproot slows down, possibly due to the fact that the roots reach unfavorable soil conditions.

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